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# Revision of the Milliped Genus *Scytonotus* Koch (Polydesmida: Polydesmidae)

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**ABSTRACT**—The milliped genus *Scytonotus* occurs in four regions of North America, one east of the Central Plains, and three west of the Continental Divide: from northern Utah to northeastern Idaho and northwestern Wyoming; from southeastern Washington and western Montana to southeastern British Columbia; and along the Pacific Coast from San Francisco Bay and the northern San Joaquin Valley to the northern extremity of the Alaskan panhandle, including all offshore islands except the Queen Charlotte Islands. Three of the nine component species occur in the East—*S. granulatus* (Say), broadly distributed across most of the area, and *S. virginicus* (Loomis) and *S. australis* Hoffman, both endemic to the Blue Ridge province. Six occur in the West—*S. insulanus* Attems and *S. bergrothi* and *simplex*, both by Chamberlin, inhabiting the Pacific Coastal region; *S. inornatus* new species, in the eastern Cascade foothills of southern Oregon; *S. columbianus* Chamberlin, in the interior of British Columbia and northeastern Washington; and *S. piger* Chamberlin, south of the International Border from Idaho to Utah. *Polydesmus amandus* Chamberlin and *S. orthodox* Chamberlin are placed in synonymy under *S. piger*, and *S. michauxi* Hoffman is reduced to a subspecies of *S. virginicus*. Taxonomic characters primarily involve the configurations of the medial, distal, and lateral laminae of the gonopodal endomerite and its length relative to the tibiotarsus. Except for *S. columbianus*, *virginicus*, and *australis*, the paranota of segments 5-9 of adult females are vestigial or absent, and the tibiae of legs 13-20/22 in males possess distal lobes on the anterior and/or caudal margins; the arrangements and sizes of the latter vary among the species and may hold taxonomic utility. Three lineages or species groups are recognized: the *granulatus* group, comprised of five species with teeth on the inner margin of the distal lamina; the *bergrothi* group, composed of three species in which the distal lamina is prolonged; and the monobasic *inornatus* group, in which the structure is unmodified. Relationships among the lineages are hypothesized as *inornatus* + (*bergrothi* + *granulatus*). Anatomical and distributional evidence point to the Cascade Mountains of southern Oregon as the primary source area, and a secondary center of evolution exists in the Blue Ridge Mountains of North Carolina and Virginia. Pertinent anatomical illustrations and distribution maps are presented along with complete synonymies, diagnoses, and a key to species.

Millipeds of the genus *Scytonotus* are common inhabitants of forests in eastern and western North America. The small, pink, tuberculate polydesmids are often encountered on the undersurfaces of wet bark, twigs, and pieces of wood, sometimes in or very close to standing water, and are more prevalent in cooler seasons of the year. *Scytonotus* is one of four disjunct diplopod genera with representatives on both sides of the continent, the other being *Ergodesmus* (Polydesmida: Nearctodesmidae), *Orinisobates* (Julida: Nemasomatidae), and *Brachycybe* (Platydesmida: Andrognathidae) (Hoffman 1962a, 1975; Gardner 1975; Enghoff 1985). *Scytonotus* occurs in four separate areas (Fig. 1): 1) the eastern United States and southern Ontario and Quebec, Canada, east of the Central Plains; 2) the Wasatch and Teton mountains, and associated ranges, of northern Utah, eastern Idaho, and western Wyoming; 3) the Rocky and Selkirk mountains, and associated ranges, of northern Idaho, western Montana, eastern Washington, and southeastern British

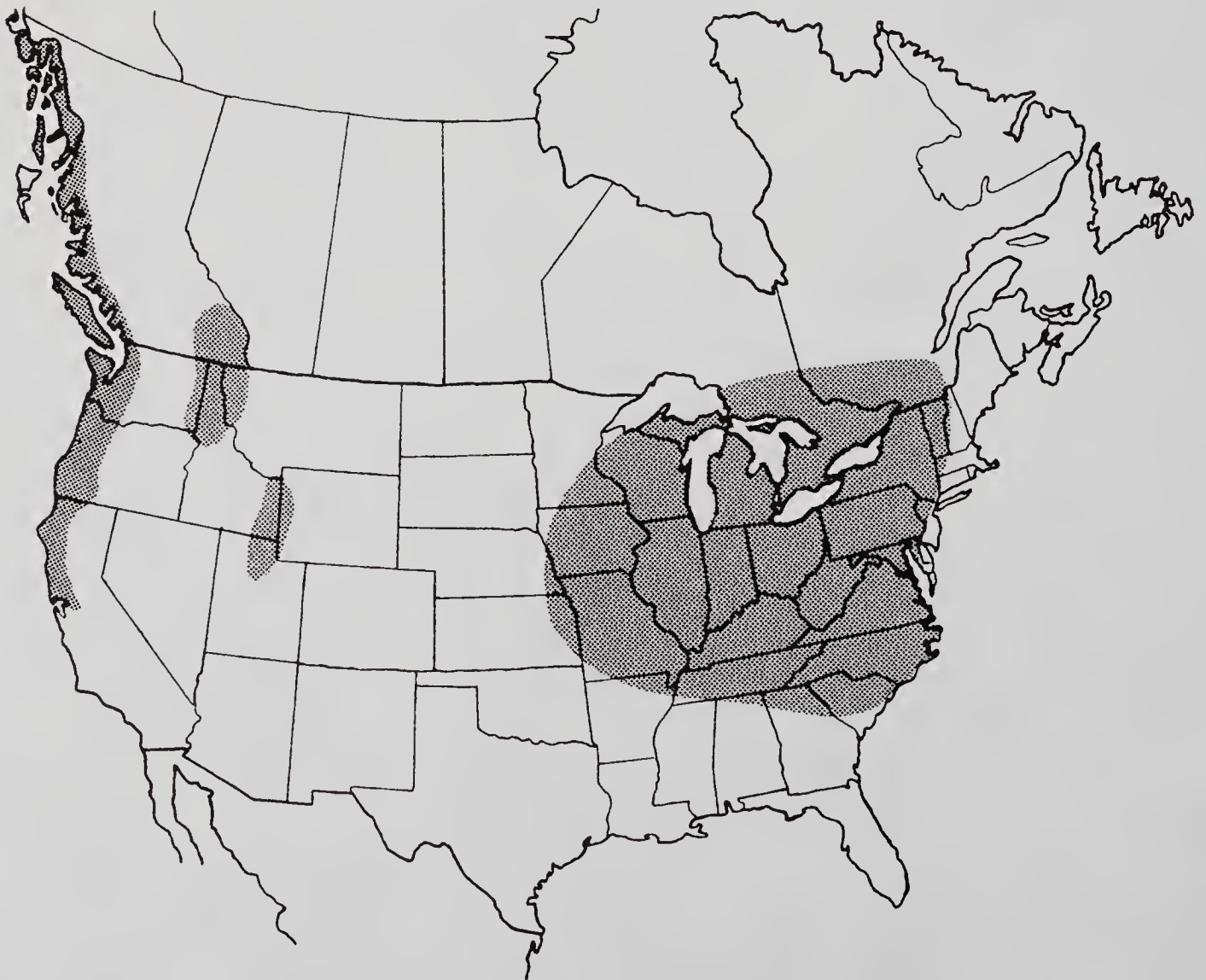


Fig. 1. Distribution of *Scytonotus*. A smooth line has been drawn around range extremes in all directions in each of the four areas.



Columbia; and 4) along the Pacific Coast extending inland to the eastern slope of the Cascade Mountains from San Francisco Bay and the northern San Joaquin Valley, California, to Yakutat Bay, Alaska, including all major offshore islands in British Columbia and Alaska except the Queen Charlotte Archipelago. The eastern fauna was reviewed by Hoffman (1962*b*), who recognized four species. One species was widespread throughout the region, *S. granulatus* (Say), and three were localized endemics in the southern Blue Ridge Province: *S. australis* and *michauxi*, both authored by Hoffman, and *S. virginicus* (Loomis). Material secured since that study shows that *S. virginicus* and *michauxi* are geographic races of a single species. As the former is the older name, *michauxi* is reduced to subspecific status. Consequently, there are only two endemic species in the Blue Ridge, *S. virginicus* and *australis*. Hoffman (1962*b*, 1979) indicated that about seven poorly known species occur in the Rocky Mountains and the Pacific Northwest of the United States and Canada, as listed by Chamberlin and Hoffman (1958), but that inadequate material precluded revision of the western fauna. With the collection of numerous samples of *Scytonotus* from the western United States and Canada in the past 30 years, a clarification of this fauna is now possible, and important new records are also available for the eastern congeners. This contribution therefore completes the study of *Scytonotus* and recognizes nine species, three in the east and six in the west. Acronyms of sources of preserved study material are as follows:

AMNH—American Museum of Natural History, New York, New York

ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania

BMNH—British Museum (Natural History), London, England

BYU—Monte L. Bean Life Science Museum, Brigham Young  
University, Provo, Utah

CADFA—California Department of Food and Agriculture, Sacramento

CAS—California Academy of Sciences, San Francisco

CIS—California Insect Survey, University of California at Berkeley

CMN—Canadian Museum of Nature, Ottawa, Ontario

CNC—Centre for Land and Biological Resources Research,  
Agriculture Canada, Ottawa, Ontario

DC—Natural Science Division, Dixie College, St. George, Utah

EIL—Zoology Department, Eastern Illinois University, Charleston

FMNH—Field Museum of Natural History, Chicago, Illinois

FSCA—Florida State Collection of Arthropods, Gainesville

GLFRS—Great Lakes Forestry Research Station, Sault Ste. Marie,  
Ontario, Canada

- ILNHS—Illinois Natural History Survey, Champaign  
 ILSU—Department of Biological Sciences, Illinois State University,  
 Normal  
 MCZ—Museum of Comparative Zoology, Harvard University,  
 Cambridge, Massachusetts  
 MNHP—Museum National d'Histoire Naturelle, Paris, France  
 NCSM—North Carolina State Museum of Natural Sciences,  
 Raleigh  
 NMNH—National Museum of Natural History, Smithsonian  
 Institution, Washington, DC  
 NMV—Naturhistorisches Museum, Vienna, Austria  
 OHS—Ohio Historical Society, Columbus  
 PSU—Frost Entomological Museum, Pennsylvania State University,  
 University Park  
 RBCM—Royal British Columbia Museum, Victoria  
 RNP—Redwood National Park, Orick, California  
 ROM—Royal Ontario Museum, Toronto  
 SDMNH—San Diego Museum of Natural History, San Diego,  
 California  
 TMM—Texas Memorial Museum, University of Texas, Austin  
 UA—Entomology Department University of Alberta, Edmonton  
 UBC—Zoology Department, University of British Columbia,  
 Vancouver  
 UCD—Bohart Entomological Museum, University of California at Davis  
 UID—Department of Plant, Soil, and Entomological Sciences,  
 University of Idaho, Moscow  
 UMMZ—University of Michigan Museum of Zoology, Ann Arbor  
 UMN—Entomology Department, University of Minnesota, St. Paul  
 USU—Biology Department, Utah State University, Logan  
 UVT—Zoology Department, University of Vermont, Burlington  
 UWBM—Thomas Burke Memorial Washington State Museum,  
 University of Washington, Seattle  
 VMNH—Virginia Museum of Natural History, Martinsville  
 WAS—Private Collection of William A. Shear, Hampden-  
 Sydney, Virginia  
 WSU—James Entomological Museum, Washington State University,  
 Pullman  
 ZMH—Zoologisches Museum, Hamburg, Germany

#### LITERATURE REVIEW

The history of *Scytonotus* begins with the description of *Polydesmus granulatus* by Say (1821) for a form from Pennsylvania, one of the first dozen millipeds named from the North Ameri-



can continent. Gervais (1847) recognized the original combination as did Wood (1865), Bollman (1893), and Kenyon (1893a). Koch (1847) erected *Scytonotus* for three new species, all now synonyms of *S. granulatus*: *S. scabricollis*, from an unspecified locality in North America, and *S. laevicollis* and *nodulosus*, both from Pennsylvania; Koch (1863) repeated these accounts. Sager (1856) proposed *Stenonia hispida* for an individual from Ann Arbor, Michigan, and Wood (1865) erected *Polydesmus setiger* for another specimen from Pennsylvania. Both names are additional synonyms of *S. granulatus* as is *S. cavernarum*, proposed by Bollman (1887) for a form from Indiana. Cook and Cook (1894) synthesized the earlier efforts and excluded five species that had been assigned to *Scytonotus* from Venezuela, New Zealand, Mexico, and the tropics. Under *S. granulatus* or a synonym, this common, eastern milliped has been recorded numerous times, and I have endeavored to list all references beside the appropriate names in the synonymy.

The second eastern species, *S. virginicus* (Loomis), type species of the genus *Lasiolathus* (Loomis 1943), was proposed for an immature specimen from Thornton Gap, Page/Rappahannock counties, Virginia. Hoffman (1947) synonymized the name with *S. granulatus* before collecting an adult male topotype and realizing (Hoffman 1950a) that *S. virginicus* is a distinct species. In his latter work, he gave the range as being the Blue Ridge Province south to Linville Falls, North Carolina. Chamberlin and Hoffman (1958) included *S. virginicus* in their checklist. Hoffman (1962b) altered the range by stating that it was unknown south of the Roanoke River and proposed the final two eastern species, *S. australis* and *michauxi*, from north Georgia and western North Carolina/eastern Tennessee, respectively.

*Scytonotus* was first recorded from western North America by Cook (1904), 83 years after Say (1821) described *P. granulatus* from the east. He reported juveniles and females of an unidentified species from Yakutat Bay, Sitka, and Juneau, Alaska, and illustrated a male from an unknown locality that he recognized as a new species. Unfortunately, Cook misplaced the specimen, so Chamberlin (1911) is credited with the authorship of *S. bergrothi* based on specimens from Bremerton, Kitsap County, Washington. Chamberlin (1910) described *S. piger* and the synonym, *Polydesmus amandus*, from Mill Creek Canyon, Salt Lake County, Utah, and 10 years later (Chamberlin 1920) added *S. columbianus* from the "Columbia Valley," British Columbia, Canada. The precise locality is unknown, but he was probably referring to the valley of the Columbia River, which arises in this Canadian province. Chamberlin (1925) proposed

*S. orthodox*, another synonym of *S. piger*, for specimens from Logan Canyon, Cache County, Utah. Attems (1931) described *S. pallidus*, a synonym of *S. bergrothi*, from Mukilteo, Snohomish County, Washington, and *S. insulanus* from Nanaimo, Vancouver Island, British Columbia. Chamberlin (1941) described *S. simplex* from Days Creek, Douglas County, Oregon.

The remaining papers covering western forms of *Scytonotus* either provided new records or summarized existing ones. Attems (1940) reviewed all the congeners, from both the east and west, transferring *amandus* into *Archipolydesmus*. Chamberlin (1943) transferred *amandus* into *Scytonotus* and recorded it from Georgetown, Bear Lake County, Idaho, the first record of the genus from this state. Causey (1954a,b) recorded *S. amandus* from Teton County, Wyoming; *S. pallidus* from Seattle, Washington; and female and immature specimens, identified only as *Scytonotus* sp., from five additional counties, one in eastern Washington. Chamberlin and Hoffman (1958) summarized all the species in their Nearctic checklist, placing *S. palidus* in synonymy under *S. bergrothi*. Hoffman (1962b) estimated that about seven species occurred from northern California and Utah to British Columbia and Alaska; he (Hoffman 1979) repeated this estimate and characterized the western range as the Rocky Mountains and west coast states. Loomis and Schmitt (1971) recorded *Scytonotus* from Montana, citing *S. amandus* from Lincoln and Mineral counties. Kevan (1983) listed all the species that were known from, or probable for, Canada, both in the east and west, and Shelley (1990) summarized the generic range in British Columbia and Alaska, giving the type localities of species in the former and misspelling *insulanus* and *insulans*.

Thus at this writing, *Scytonotus* consists of the following species, listed chronologically below with their type localities and other reported occurrences:

*S. granulatus* (Say 1821). Vicinity of Philadelphia, Pennsylvania. Also recorded from Canada in general (Wood (1865), Ontario (Causey 1952, Hoffman 1962b, Judd 1967, Kevan 1983, Shelley 1988), and the following states: New York (Cook and Cook 1894, Bailey 1928, Chamberlin and Hoffman 1958, Hoffman 1962b, Kevan 1983), Pennsylvania (Gervais 1847; Koch 1847, 1863; Wood 1865; Cook and Cook 1894; Dearolf 1938; Loomis 1939; Attems 1940; Chamberlin 1947, Chamberlin and Hoffman 1958; Hoffman 1962b; Kevan 1983), Maryland (Hoffman 1962b), District of Columbia (Cook and Cook 1894), West Virginia (Hoffman 1962b), Virginia (Cook and Cook 1894; Hoffman 1947, 1950a, 1962b), North Carolina (Brimley 1938; Chamberlin 1940; Hoffman 1950b, 1962b; Chamberlin and Hoffman



1958; Wray 1967; Shelley 1978; Filka and Shelley 1980), Michigan (Sager 1856, Wood 1865, Bollman 1888*b*, Cook and Cook 1894, Johnson 1954, Hoffman 1962*b*, Kevan 1983), Ohio (Morse 1902, Williams and Hefner 1928, Kevan 1983), Indiana (Bollman 1887, 1888*a*, 1893; McNeill 1888; Cook and Cook 1894; Attems 1940; Chamberlin 1952; Chamberlin and Hoffman 1958; Hoffman 1962*b*), Kentucky (Causey 1955, Loomis 1944, Hoffman 1962*b*), Tennessee (Bollman 1888*b*, Hoffman 1962*b*), Illinois (Rapp 1946, Chamberlin 1952, Hoffman 1962*b*), Minnesota (Bollman 1893, Hoffman 1962*b*, Kevan 1983), Iowa (Chamberlin 1942, Chamberlin and Hoffman 1958, Hoffman 1962*b*), Missouri (Chamberlin 1928, Chamberlin and Hoffman 1958, Hoffman 1962*b*), Nebraska (Kenyon 1893*a,b*), and Kansas (Gunthrop 1913).

*S. piger* Chamberlin 1910. Mill Creek Canyon, Salt Lake County, Utah. Also recorded from the Wasatch Mountains, Utah (Chamberlin and Hoffman 1958).

*S. amandus* (Chamberlin 1910). Mill Creek Canyon, Salt Lake County, Utah. Also recorded from Georgetown, Bear Lake County, Idaho (Chamberlin 1943), Teton County, Wyoming (Causey 1954*a*), the Wasatch Mountains of Utah (Chamberlin and Hoffman 1958), and Lincoln and Mineral counties, Montana (Loomis and Schmitt 1971).

*S. bergrothi* Chamberlin 1911. Bremerton, Kitsap County Washington. Also recorded from Port Ludlow, Jefferson County; Tacoma, Pierce County; Mukilteo, Snohomish County; and Port Blakeley, Kitsap County, Washington (Attems 1931, Chamberlin and Hoffman 1958), and Seattle, King County, Washington (Causey 1954*b*).

*S. columbianus* Chamberlin 1920. "Columbia Valley," British Columbia, Canada, probably the valley formed by the Columbia River; also recorded from this site by Chamberlin and Hoffman (1958) and Shelley (1990).

*S. orthodox* Chamberlin 1925. Logan Canyon, Cache County, Utah. Also recorded from Coeur d'Alene, Kootenai County, Idaho, and the Bear Lake region of Idaho and Utah (Chamberlin and Hoffman 1958).

*S. insulanus* Attems 1931. Nanaimo, Vancouver Island, British Columbia, Canada. Also recorded from Juneau, Alaska (Chamberlin and Hoffman 1958).

*S. simplex* Chamberlin 1941. Day's Creek, Douglas County, Oregon.

*S. virginicus* (Loomis 1943). Thornton Gap, Page/Rappahannock counties, Virginia. Also reported from Sugar Hollow, Albemarle County, and Humpback Mountain, Nelson County, Virginia (Hoff-

man 1950a, 1962b), and Peaks of Otter, Bedford County, Virginia (Hoffman 1962b).

*S. australis* Hoffman 1962b; 6 mi (9.6 km) W Amicalola Falls, Dawson County, Georgia. Also known from White County, Georgia (Hoffman 1962b).

*S. michauxi* Hoffman 1962b. Roan Mountain, Carver County, Tennessee. Also known from two other sites in Carter County and sites in Ashe, Avery, Buncombe-Transylvania, Macon, Mitchell, and Yancey counties, North Carolina (Hoffman 1962b).

### TAXONOMIC CHARACTERS

The taxonomically important features of *Scytonotus* chiefly involve aspects of the male gonopods, but as noted by Cook and Cook (1894), certain nonsexual features provide clues to a form's identity and, in a few cases when combined with geography, a reliable determination. The genus is distinguished by two branches to the gonopod telopodite, the dentate paranota, and the flattened to lowly rounded, setiferous, dorsal tubercles that occur in relatively linear transverse rows. Species of *Scytonotus* are pink in color as is *Bidentogon*, a sympatric polydesmid genus occurring around San Francisco Bay (Shear 1972); it and trichopolydesmids also exhibit setose, tuberculate dorsums and can thus be confused with *Scytonotus*. However, their setae are stiffer and more noticeably clavate, and their tubercles are higher, more subconical, and more strongly elevated above the dorsum and delineated from each other. Consequently, they differ from *Scytonotus*, which has a softer, "fuzzier" appearance, and adult trichopolydesmids, pallid in color, are also much smaller and narrower in proportion to their lengths. Though not sympatric with *Scytonotus*, *Harpagonopus*, occurring along the Pacific Coast of southern California and northern Baja California Norte, is also pink and dorsally setose and tuberculate (Loomis 1960, Shelley 1993), and at first glance appears to be *Scytonotus*. However, the setae of its sole species, *H. confluentus* Loomis, also are stronger, stouter, and more clavate than those of *S. simplex*, the most proximate species of *Scytonotus*. In addition, the dorsal tubercles are more strongly demarcated from each other, as opposed to the lower, less pronounced ones of *S. simplex*. These attributes impart an almost velveteen appearance to specimens of *Scytonotus*, particularly juveniles, and with practice one can learn to distinguish this genus from phenotypically similar forms from California and Oregon with which it is often mixed in the same sample.

*Scytonotus* can also be recognized by the tibial lobes on legs 13–20/22 of most adult males and the reduced paranota on seg-



ments 5–9 of most adult females. Hoffman (1962*b*) correctly observed that the species in the Blue Ridge Province have normal paranota in adult females and lack tibial lobes in males, which distinguish them from *S. granulatus* in areas where their ranges abut near the Blue Ridge Province. Likewise, *S. columbianus* lacks the lobes in males and has normal paranota in females, allowing it to be distinguished from *S. piger* in the interior of British Columbia and the adjacent part of the United States. Details of the tibial lobes, paranota, and taxonomically important aspects of the gonopods are provided in the ensuing paragraphs. The species diagnoses in the descriptive accounts cite, in sequence, the attributes of the male tibiae; the relative lengths of the gonopodal tibiotarsi and endomerites; the characteristics of the medial, distal, and lateral laminae of the gonopods; and the condition of the paranota on segments 5–9 in females.

*Tibia of legs 13–20/22 in males*—As noted by Cook and Cook (1894), several leg articles are enlarged and papillose to varying degrees, but these traits are difficult to see, do not appear to hold taxonomic utility, and are not treated here. However, the tibiae of legs 13–20/22 (the posterior legs of segment 9 through the posterior legs of segment 13/anterior legs of 14) are modified in all species except *S. columbianus*, *virginicus*, and *australis*. The tibiae on these legs are swollen ventrally and possess one or two distal lobes on the caudal, anterior, or both margins. The lobes arise suddenly on the 13th tibiae as long, subterminal projections from the caudal margins (Fig 2). They are glabrous and laminate, curve slightly, extend beyond the distal extremities of the podomeres, and are broad apically. The pattern varies (Table 1), but in general this configuration persists through the 16th legs (anterior legs of segment 11). On the 17th legs (caudal legs of the 11th segment) there is a smaller, moderate-size lobe in the same position. On the 18th legs of most species, the anterior legs of segment 12, there is a small lobe at this position and one directly opposite on the anterior margin (Fig. 3). Depending on the species, the anterior lobe persists through the 20th/22nd tibiae, while the caudal lobe disappears. The anterior lobe also disappears after legs 20/22, and the remaining legs are unmodified.

Cook and Cook (1894) stated that legs 13–20 in *S. granulatus*, the ones with tibial modifications, clasp the segments of females with reduced paranota during copulation. No evidence was provided, but five segments are involved in females, numbers 5–9, and the legs on five or six segments (segments 9–13/14) are modified in males, so the statement is plausible because the modifications corre-

late. Segment 7 of the male, the copulatory segment, must align with segment 3, the reproductive segment of the female, which places the first modified segments, 9 of the male and 5 of the female, opposite each other. Because of this correlation, it is not surprising that the species that lack one modification also lack the other, as is the case with *S. columbianus*, *virginicus*, and *australis*. Consequently, the presence or absence of these modifications is taxonomically important in the northern Rocky Mountains and the Blue Ridge Province (Figs. 10, 30), as they enable accurate determinations of *S. columbianus* versus *S. piger*, and *S. granulatus* versus *S. virginicus* or *australis*.

In spot checking males of each species with lobes, I noted that the number of leg pairs, the sequence of large versus small lobes, and the occurrence of anterior lobes vary among species. Table 1 shows the legs that are modified in the species possessing lobes; they are absent from the anterior or caudal margins where no size is indicated. This variation may hold taxonomic utility, particularly for determining males when the gonopods are lost.

*Segments 5–9 in females*—In all species except *S. columbianus*, *virginicus*, and *australis*, the paranota on segments 5–9 of adult females are reduced or absent, resulting in a distinctly narrower,

Table 1. Comparison of Tibial Lobes of Adult Males of *Scytonotus* spp.<sup>1</sup>

Segment Number	9		10		11		12		13		14	
Leg Number	13	14	15	16	17	18	19	20	21	22	23	
<i>piger</i>	a -	a -	a -	a -	a -	a - s	a - s	a - m				
	c -	c - s	c - s	c - s	c - s	c - s	c - s	c -				
<i>insulanus</i>	a -	a -	a -	a -	a -	a - s	a - s	a - s	a - s	a - s		
	c - l	c - l	c - l	c - m	c - m	c - m	c - s	c - s	c - s	c -	c -	
<i>bergrothi</i>	a -	a -	a -	a -	a -	a - s	a - m	a - m	a - m			
	c - l	c - l	c - l	c - l	c - m	c - m	c - m	c - m	c -			
<i>simplex</i>	a -	a -	a -	a -	a -	a - s	a - s	a - s				
	c - l	c - l	c - l	c - l	c - l	c - s	c - s	c -				
<i>inornatus</i>	a -	a -	a -	a -	a -	a - s	a - s	a - s				
	c - l	c - l	c - l	c - l	c - s	c - s	c - s	c - s				
<i>granulatus</i>	a -	a -	a -	a - l	a - s	a - l	a - l					
	c - l	c - l	c - l	c - l	c - m	c - s	c - s	c -				

<sup>1</sup> Symbols in the table are:  
a –condition of anterior tibial margin  
c –condition of caudal tibial margin  
l –large lobes (Fig. 2)  
s –small lobes (Fig. 3)  
m –moderate lobes, an intermediate conditon or small version of the large configuration



cylindrical shape to this part of the body. The paranota are vestigial on segments 5 and 9 and are absent from segments 6–8. The distinction applies only to adults; I have examined innumerable juvenile females of different sizes, and presumably different instars, with well developed paranota on these segments. Loss of these structures thus appears to occur at the final molt and to coincide with the attainment of sexual maturity.

*Male gonopods*—As in all polydesmids, the most important taxonomic features in *Scytonotus* are located on the gonopodal telopodite, which consists of two branches that join basally. I adopt the system of Attems (1940) and Golovatch (1991) and label the blade-like, anterior projection as the “tibiotarsus” and the variable caudal structure with a pulvillus on the inner margin as the “endomerite.” Three laminae arise from the endomerite stem, one each on the medial and lateral sides and one distad. The principal taxonomic characters involve the relative lengths of the tibiotarsi and the endomerites as well as the sizes and configurations of the three lamellae.

*Medial lamina*—The medial lamina arises proximally on the endomerite, often proximal to the pulvillus, extends for varying lengths along the stem, and usually terminates before the modifications of the distal lamina. In most species the medial lamina expands basally into a variable lobe or flange that may overhang and partly obscure the inner margin of the endomerite. Distally it varies greatly, tapering smoothly onto the endomerite in *S. piger*, *columbianus*, *inornatus*, and *granulatus* (Figs. 5, 7, 17, 21), and terminating in one or more variable teeth or spurs in *S. insulanus*, *bergrothi*, *simplex*, *virginicus*, and *australis* (Figs. 11, 13, 15, 23, 25, 27).

*Distal lamina*—The distalmost part of the endomerite, the distal lamina arises at varying points along the stem beginning near midlength. There are three basic configurations: with two or three teeth on the inner margin, as in *S. piger*, *columbianus*, *granulatus*, *virginicus*, and *australis* (Figs. 5–8, 21–28); expanded basally into a small lobe or spur and prolonged distad to varying degrees, thus extending beyond the distal extremity of the tibiotarsus, as in *S. insulanus*, *bergrothi*, and *simplex* (Figs. 11–16); and unmodified, as in *S. inornatus* (Figs. 17–18).

*Lateral lamina*—Like its medial counterpart, the lateral lamina arises at various points along the endomerite stem, in some species proximal to the pulvillus, and usually terminates proximal to the modifications of the distal lamella. The structure is long, slender, and unmodified in *S. piger*, *columbianus*, *inornatus*, and *australis* (Figs. 6, 8, 18, 28); expands into rounded lobes in *S. insulanus* and *bergrothi* (Figs. 12, 14); possesses a subspiniform projection in

*S. virginicus* (Figs. 24, 26); and is expanded with one or two marginal teeth in *S. granulatus* (Fig. 22). The most intricate structure occurs in *S. simplex*, where the lamina expands basally into a lightly serrate lobe, narrows at midlength, and possesses a short spur around 2/3 length (Fig. 16).

### Genus *Scytonotus* Koch

*Scytonotus* Koch, 1847:57. Bollman 1893:122,141–142. Cook and Cook, 1894:233–235. Cook, 1904:61. Williams and Hefner, 1928:111. Attems, 1898:255–256; 1931:144–145; 1940:155. Hoffman, 1950a:219–250; 1962b:242; 1979:173. Causey, 1955:22. Chamberlin and Hoffman, 1958:72. Jeekel: 1971:351. Kevan, 1983:2969.

*Lasiolathus* Loomis, 1943:318–319. Jeekel, 1971:334.

*Type species*—Of *Scytonotus*, *S. scabricollis* Koch, by subsequent designation of Bollman (1893). Hoffman (1962b) states that designation was by Chamberlin and Hoffman (1958), but as noted by Jeekel (1971), it actually dates to Bollman (1893:151). Of *Lasiolathus*, *L. virginicus* Loomis, by original designation.

*Diagnosis*—Small polydesmids with four to five rows of rounded, setose tubercles dorsally on metatergites; adults with 19 segments; dorsum moderately convex; paranotal margins shallowly notched or deeply dentate, those of segments 5–9 of females of most species vestigial or absent; tibiae of legs 13–20/22 of males of most species swollen ventrad and with variable, elongate, subterminal lobes on anterior and/or caudal margins; telopodite of male gonopod with or without one or two barbed, aciculate projections proximally on medial surface, with elongate tibiotarsus arising basally anterior to endomerite, latter with basal pulvillus on caudal surface and variably dentate medial, distal, and lateral laminae; prostatic groove internal, with distal loop, opening at pulvillus.

*Distribution*—Occurring in four separate faunal regions, one east and three west of the Continental Divide (Fig. 1). In the East, *Scytonotus* covers a large, continuous area east of the Central Plains extending from near Sault Ste. Marie, Ontario, and Trois Rivières, Quebec, to southcentral South Carolina, north Georgia, and northeastern Arkansas; east–west, this area spreads from eastern Vermont, coastal Virginia, and the Outer Banks of North Carolina to eastern Kansas and Nebraska. In the West, *Scytonotus* occurs along the Pacific Coast and in two areas in the interior. The coastal area extends from Yakutat Bay, Alaska, to Marin and San Joaquin counties, California, extending inland to the eastern slope of the Cascade Mountains in Oregon and Washington, and includes all intervening offshore islands in British Columbia and Alaska except the Queen



Charlotte Islands, where it never has been encountered. In the interior, *Scytonotus* occurs in the Columbia River Valley and the Rocky and Selkirk mountains, and associated ranges, from Revelstoke and Yoho National Parks, British Columbia, to southeastern Washington, western Montana, and the southern extremity of the Idaho Panhandle near the Salmon River. It is also known in the Wasatch and Teton mountains, and associated ranges, in western Wyoming, eastern Idaho, and northern Utah south to Salt Lake County.

*Species*—Nine, three in eastern North America, one divided into two geographic races, and six in the west. The species are arranged into three lineages or species groups, which are named for the oldest component.

Key to Species of *Scytonotus*, based on adult males

- 1. Distal lamina of gonopodal endomerite with 2 or 3 distal teeth (Figs. 5-8, 21-28) ..... 2  
Distal lamina otherwise ..... 6
- 2. Medial lamina with 2 distinct teeth (Figs. 23, 25); Warren County, Virginia, to Sevier County, Tennessee, and Swain County, North Carolina ..... *virginicus* (Loomis)  
Medial lamina with 1 or no teeth, with or without a rounded, basal lobe or flange ..... 3
- 3. Distal lamina with 3 teeth, the apical one much smaller and preceded by 2 larger, subequal teeth (Fig. 21); Ontario and Quebec to South Carolina, Tennessee, Arkansas, and Kansas ..... *granulatus* (Say)  
Distal lamina with 2 subequal teeth ..... 4
- 4. Medial lamina with distinct distal tooth (Fig. 27); Buncombe County, North Carolina, and Sevier County, Tennessee, to Oconee County, South Carolina, and Dawson County, Georgia ..... *australis* Hoffman  
Medial lamina with variable basal lobe but without distal tooth ..... 5
- 5. Endomerite much shorter than tibiotarsus; medial lamina a short, narrow flange, not overhanging inner margin of endomerite (Fig. 7); interior of British Columbia and northeastern Washington ..... *columbianus* Chamberlin

- Endomerite subequal in length to tibiotarsus; medial lamina longer, with rounded basal lobe overhanging and partly obscuring inner margin of endomerite (Fig. 5); north-eastern Washington, northern Idaho, and western Montana to Salt Lake County, Utah ..... *piger* Chamberlin
6. Endomerite subequal in length to tibiotarsus, distal lamina without modifications, not prolonged, inner margin smooth, entire (Fig. 17); Klamath County, Oregon ..... *inornatus*, new species  
Endomerite longer than tibiotarsus, inner margin of distal lamina variously modified and prolonged, with or without teeth..... 7
7. Distal lamina apically divided, medial part thin and narrow, greatly prolonged and strongly decurved, without teeth (Fig. 11); Yakutat Bay, Alaska, to Douglas County, Oregon, and Whitman County, Washington ..... *insulanus* Attems  
Distal lamina not divided, slightly to moderately prolonged, only slightly decurved ..... 8
8. Distal lamina directed at about a right angle from endomerite stem, slightly prolonged and expanded basally into narrow lobe, without teeth; medial lamina narrowing greatly distad, with short apical tooth, not overhanging endomerite stem (Fig. 15); Lincoln County, Oregon, to Marin and San Joaquin counties, California ..... *simplex* Chamberlin  
Distal lamina curving gently away from tibiotarsus, moderately prolonged, with sharply acute basal tooth, without lobes, medial lamina greatly expanded distad, with apical tooth, overhanging and obscuring inner margin of endomerite (Fig. 13); southern British Columbia to Douglas County, Oregon ..... *bergrothi* Chamberlin

THE WESTERN SPECIES

The *Granulatus* Group

The most speciose lineage in *Scytonotus*, the *granulatus* group occurs in the eastern region and both areas in the western interior and is absent from the Pacific Coast. It is characterized primarily by the presence of two or three teeth, usually subequal in size, on



the inner margin of the distal lamina. The medial lamina varies in length and is typically expanded into a basal lobe or flange, except on the Blue Ridge endemics, which have one or two distinct teeth. The lateral lamina is long, slender, and generally unmodified, except for *S. granulatus* and *virginicus*, in which the structure also has one or two teeth. Finally, the endomerite is shorter than or subequal in length to the tibiotarsus. The Blue Ridge species and *S. columbianus* have normal paranota on all segments in females, and males lack the tibial lobes. However, because all other congeners possess reduced paranota in females and lobes in males (Table 1), I regard the conditions in these three species as apomorphies representing secondary simplification rather than plesiomorphies, and the similarity between *S. columbianus* and *S. virginicus/australis* represents convergence. Spatial distributions tend to be allopatric and parapatric, with only minimal sympatry between *S. virginicus michauxi* and *australis*, in the Great Smoky Mountains, and between *S. piger* and *columbianus*, in northwestern Washington. Relationships among the components are hypothesized as *columbianus* + (*piger* + (*granulatus* + (*virginicus* + *australis*))) (Fig. 34). The Blue Ridge Province seems to be a secondary center of evolution after the presumptive primary source area in the Cascade Mountains. The western representatives of the *granulatus* lineage are detailed below; the eastern species are characterized at the conclusion of the descriptive section.

*Components*—*granulatus* (Say), *piger* Chamberlin, *columbianus* Chamberlin, *virginicus* (Loomis) (v. *virginicus*, v. *michauxi* Hoffman), *australis* Hoffman.

*Scytonotus piger* Chamberlin

Figs. 2–6

*Scytonotus piger* Chamberlin, 1910:244–245, pl. 36, figs. 1–5. Attems, 1940:159. Chamberlin and Hoffman, 1958:73.

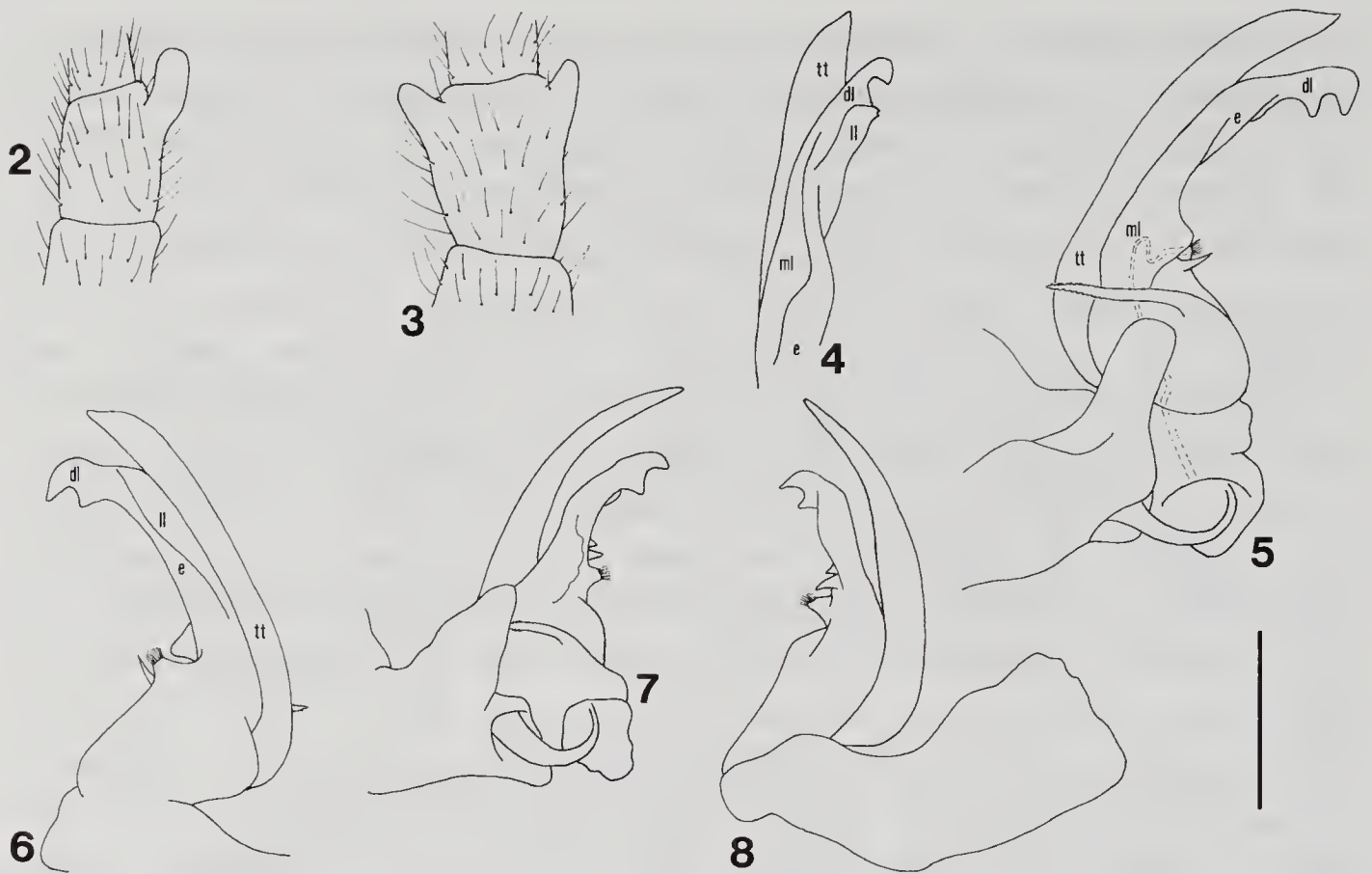
*Polydesmus amandus* Chamberlin, 1910:249–250, pl. 38, fig. 6, pl. 39, fig. 1. NEW SYNONYMY.

*Scytonotus orthodox* Chamberlin, 1925:61. Attems, 1940:159. Chamberlin and Hoffman, 1958:73. Kevan, 1983:2969. NEW SYNONYMY.

*Archipolydesmus amandus*: Attems, 1940:154–155. fig. 226.

*Scytonotus amandus*: Chamberlin, 1943:143. Causey, 1954:223. Chamberlin and Hoffman, 1958:72. Loomis and Schmitt, 1971:117. Kevan, 1983:2969.

*Type specimens*—One male and one female syntype (NMNH) taken by an unknown collector on an unknown date in the upper reaches of Mill Creek Canyon, Salt Lake County, Utah.



Figs. 2–8. 2–6, *S. piger*. 2, tibia of leg 13 of male from Teton County, Wyoming. 3, tibia of leg 17 of male from Mineral County, Montana, 4, distal extremity of telopodite of male from Mineral County, Montana, dorsal view. 5, left gonopod of male from Teton County, Wyoming, medial view. 6, the same, lateral view. 7–8, *S. columbianus*. 7, left gonopod of paratype, medial view. 8, the same, lateral view. dl, distal lamina; e, endomerite; ll, lateral lamina; ml, medial lamina; tt, tibiotarsus. Scale line = 0.5 mm for all figures.

**Diagnosis**—Tibiae of legs 13–20 in males with distal lobes on anterior and/or caudal margins (Figs. 2–3); endomerite subequal in length and closely appressed to tibiotarsus; medial lamina extending for about half the length of endomerite, with short but broad basal lobe, overhanging and obscuring inner margin of endomerite; distal lamina with two blunt teeth; lateral lamina extending for about 2/3 of length of endomerite, expanding slightly distad, with or without small marginal spurs, not overhanging margin of stem (Figs. 4–6); paranota of segments 5–9 reduced in females.

**Variation**—There are slight differences among the male gonopods that do not conform to a geographic pattern. The lobe on the medial lamina is located slightly distal to the pulvillus on a few males, and the spur proximal to the latter is absent from other. The teeth on the distal lamina are greatly reduced in individuals from Box Elder County, Utah, where they are more like small, rounded lobes, and the lateral lamina is expanded with slight marginal spurs in a few males from northern Idaho and western Montana (Fig. 4).



*Ecology*—According to labels with preserved samples, *S. piger* has been taken from the following microhabitats: aspen logs and litter, mixed lodgepole pine and fir litter, mixed aspen and fir litter, moss on logs and stumps, big-toothed maple detritus, chokeberry duff, juniper litter, mixed yellow pine and fir litter, birch duff, and fern duff. In Montana, Loomis and Schmitt (1971) collected it from moist moss by a stream; red cedar, larch, white pine, and spruce litter; and under rocks by a creek in a lodgepole pine forest.

*Distribution*—Occurring in two allopatric populations separated by approximately 274 mi (438 km), one in the Rocky Mountains of northeastern Washington, northern Idaho, and western Montana, and the other in the Wasatch and Teton mountains, and associated ranges, of eastern Idaho, western Wyoming, and northern Utah as far south as Salt Lake County (Figs. 9–10). Specimens were examined as follows:

MONTANA: *Flathead Co.*, Columbia Falls, 16 juvs., 20 August 1966, D. R. Miller (UCD). *Lincoln Co.*, 8.5 mi (13.6 km) E Libby, 3 juvs., 29 July 1958, C. C. Hoff (AMNH); and Bull L. Cpgd., M. 5F, 2 May 1965, R. Schmitt (FSCA). *Mineral Co.*, 10 mi (16 km) S, 3 mi (4.8 km) W Superior, 4 juvs., 13 September 1978, A. K. Johnson (NCSM); and 10.5 mi (16.8 km) S, 3.5 mi (5.6 km) W Superior, along Trout Cr., 2M, 3 September 1978, A. K. Johnson (NCSM).

WASHINGTON: *Stevens Co.*, Abercrombie Mtn., ca. 14 mi (22.4 km) E Northport, 48.927°N, 117.458°W, M, 3 September 1980, R. Crawford (UWBM).

IDAHO: *Bonner Co.*, E of Kootenai, entrance U. ID. field sta., 2F, 11 August 1991, R. M. Shelley (NCSM). *Kootenai Co.*, Coeur d'Alene, 6M, 4F, 3 juvs., 4 September 1949, S. Mulaik (NMNH). *Latah Co.*, 4 mi (6.4 km) N, 8 mi (12.8 km) E Harvard, Banks Gulch, M, 2 juvs., 16 September 1977, and 7 juvs., 15 September 1978, A. K. Johnson (NCSM); 8 mi (12.8 km) NE Harvard, 2M, 11F, 9 June 1982, R. S. Zack (WSU); and S. slope Moscow Mtn., M, 3F, 3 October 1964, R. L. Westcott (UCD). *Clearwater Co.*, 9.7 mi (15.5 km) W, 6 mi (9.6 km) S Pierce, M, F, 15 August 1978, A. K. Johnson (NCSM). *Fremont Co.*, 2 mi (3.2 km) N Warm River, 4 juvs., 12 August 1959, C. C. Hoff (AMNH). *Bear Lake Co.*, Georgetown, MM, FF, 17 August 1931, W. J. Gertsch (NMNH); Pineview, 6M, 14 August 1940, W. Ivie, (NMNH); Montpelier, Emigration Cyn., MM, FF, juvs., 17 August 1931, W. J. Gertsch (NMNH); 9 mi (14.4 km) NW Ovid, 5 juvs., 4 August 1959, C. C. Hoff (AMNH); and 13 mi (20.8 km) SW Ovid, F, 6

June 1984, J. B. Johnson, F. W. Merickel (UID). *Franklin Co.*, Cub R. Cyn., Wasatch Mts., M, 2F, 7 juvs., 4 July 1952, 12 October 1963, and 8–18 May 1969, G. F. Knowlton (ILNHS, NMNH). *Oneida Co.*, 11.6 mi (18.6 km) SW Downey, Summit Forest Camp, 2M, 4 September 1966, G. E. Ball, D. R. Whitehead (VMNH).

WYOMING: *Teton Co.*, Grand Teton Natl. Pk., Sunset L., Alaska Basin, juv., 29 July 1961, J. G. Edwards (FSCA); Wilson, 2M, 4 juvs., 20 August 1979, A. G. Grubbs (TMM); 12 mi (19.2 km) W Jackson, 3 juvs., 7 August 1959, C. C. Hoff (AMNH); 9 mi (14.4 km) W Jackson, 5 juvs., 5 August 1959, C. C. Hoff (AMNH); 21 mi (33.6 km) SE Jackson, along hwys. 187/189, juv., 6 August 1949, C. C. Hoff (AMNH). *Sublette Co.*, 28 mi (44.8 km) SE Jackson, along US hwys. 187/189, 8 juvs., 6 August 1959, C. C. Hoff (AMNH). *Lincoln Co.*, Cyn. E. Bedford, F, 2 juvs., 27 June 1962, W. Ivie (AMNH); nr. Afton, M, F, 19 August 1931, W. J. Gertsch (NMNH); and 4 mi (6.4 km) S Alpine Jct., juv., 27 August 1991, R. M. Shelley (NCSM).

UTAH: *Rich Co.*, Bear Lake, 2M, 2F, 2 juvs., 9 September 1919, R. V. Chamberlin (NMNH); and West Hodges Cyn., MM, FF, juvs., 7 June 1975–29 October 1976, G. F. Knowlton (MCZ). *Cache Co.*, Tony Grove Cyn., M, 2 September 1977, G. F. Knowlton (MCZ); Blacksmith Fork Cyn., M, 5 November 1966, G. F. Knowlton (NMNH); Logan Cyn., 15 juvs., 2 July 1927, R. V. Chamberlin (NMNH), 2F, 29 October 1952, G. F. Knowlton (NMNH), 3F, 11 April 1959, G. F. Knowlton (AMNH), 2F, juv., 14 May 1959, G. F. Knowlton (USU), M, 10 juvs., 17–29 November 1966, G. F. Knowlton (NMNH), M, F, 27 May 1970 (WAS), 14 juvs., 7 July 1970, G. F. Knowlton (UCD), 4M, 2F, 26 October 1977, G. F. Knowlton (MCZ), 4M, F, juv., date unknown, R. V. Chamberlin (NMNH), and MM, FF, 1 November 1976–20 May 1978, G. F. Knowlton (MCZ); Green Cyn., M, 22 May 1968, G. F. Knowlton (NMNH), 2F, 27 April 1974, G. F. Knowlton (USU), and MM, FF, 29 October 1977, G. F. Knowlton (MCZ); Smithfield Cyn., M, juv., 27 April 1968, G. F. Knowlton (NMNH); Wellsville Cyn., M, 6F, 2 juvs., 25 May 1970, G. F. Knowlton (WAS); and Logan, Spring Hollow, F, 6 April 1959, R. Amoreaux (USU). *Box Elder Co.*, Wellsville Mts., site not specified, 7 juvs., 22 June 1956, G. F. Knowlton (CIS) and Cold Spring, 2 juvs., 19 June 1968, G. F. Knowlton (NMNH); and Box Elder Cyn., M, 12 November 1968, G. F. Knowlton (NMNH). *Weber Co.*, Ogden Cyn., 12M, 10F, 7 May 1927, R. V. Chamberlin (NMNH). *Salt Lake Co.*, Salt Lake City, City Cr. Cyn., 10M, 2F, 3 juvs., 11 September 1931, W. J. Gertsch (NMNH), Rotary Pk., M, 4F, 11 and 16 September 1942,



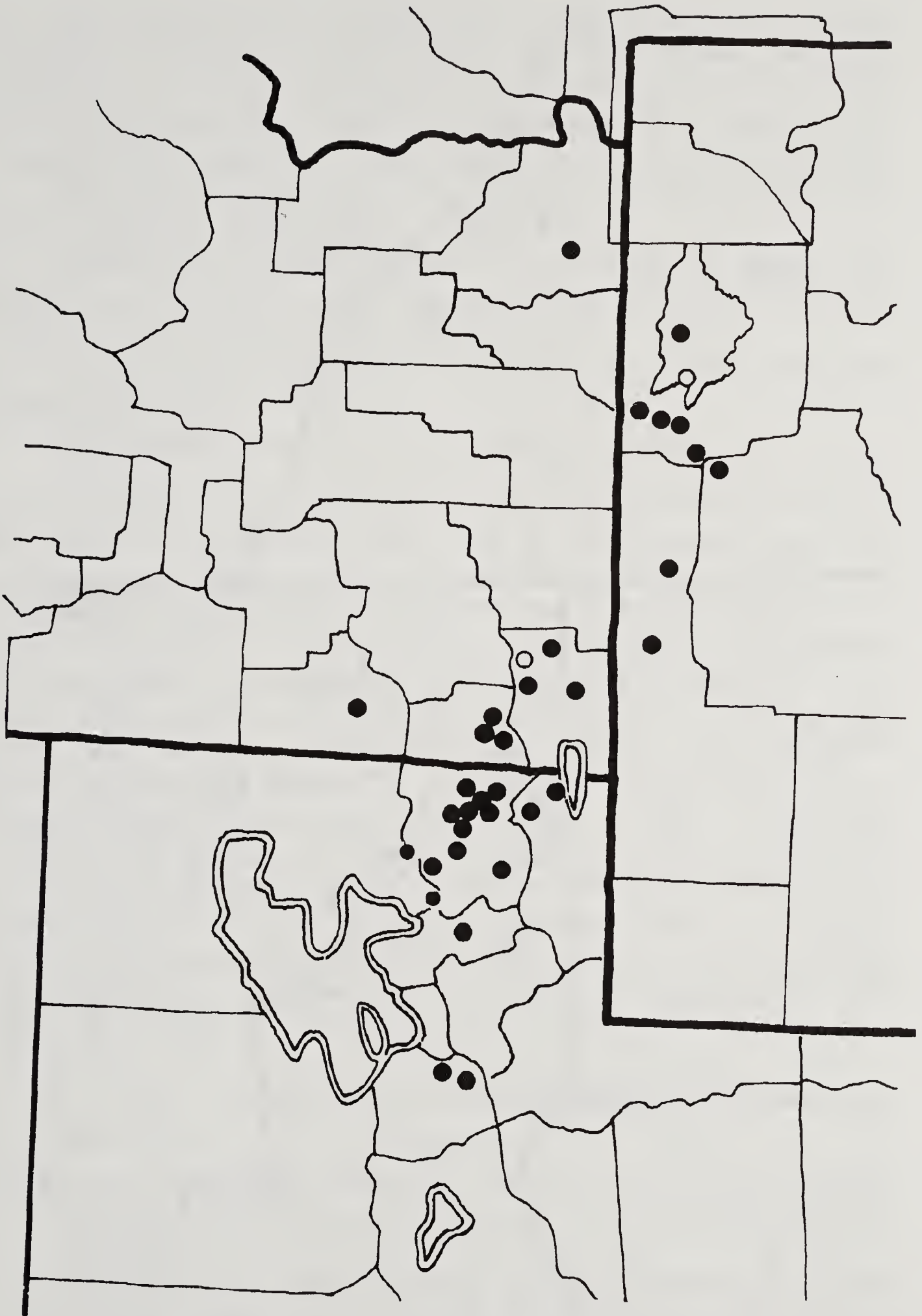


Fig. 9. Distribution of *S. piger* in eastern Idaho, western Wyoming, and northern Utah.

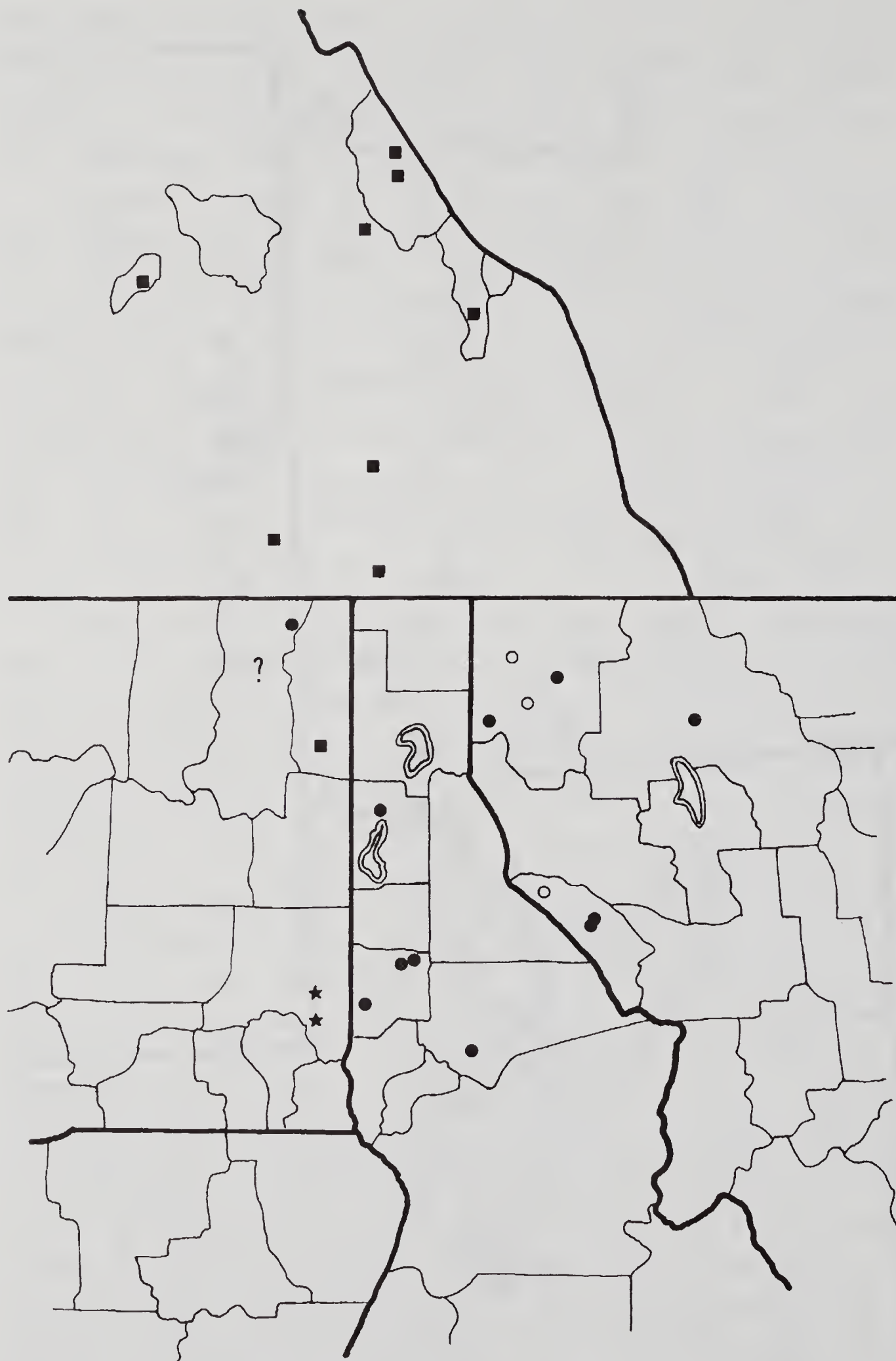


Fig. 10. Distributions of *S. piger* (dots), *columbianus* (squares), and *insulanus* (stars) in eastern Washington, northern Idaho, western Montana, and southeastern British Columbia. Circles denote literature records of *S. piger* deemed reliable; the question mark denotes a literature record of *Scytonotus* sp. (Causey 1954b) that could be either *S. piger* or *columbianus*.



W. Ivie (NMNH), Ft. Douglas, F, 17 July 1951, Y. M. Wang (NMNH), and Mill Cr. Cyn., M, F, date and collector unknown (NMNH), and F, date unknown, R. V. Chamberlin (NMNH) TYPE LOCALITY; and Lamb Cyn., F, 20 September 1930, collector unknown (NMNH) and juvs., 21 July 1942, S. and D. Mulaik (NMNH).

The following literature records are also deemed reliable and are designated by open symbols in figs. 9–10.

MONTANA: *Lincoln Co.*, 8.5 mi (13.6 km) W Libby, and along Zulu Cr., S Fork Yaak R. (Loomis and Schmitt 1971). *Mineral Co.*, Saltese (Loomis and Schmitt 1971).

IDAHO: *Bear Lake Co.*, 7 mi (11.2 km) NW Georgetown (Chamberlin 1943).

WYOMING: *Teton Co.*, Moose (Causey 1954a).

*Remarks*—With two teeth each on the distal laminae, *S. piger* and *columbianus* are very similar. I have seen only three males of the latter, so my concepts may need to be modified when more specimens are available. From this material, the endomerite and tibiotarsus are consistently subequal in length, closely appressed together, and overlap basally in *S. piger*, whereas in *S. columbianus*, the endomerite is much shorter and widely separated from the tibiotarsus (Figs. 5–8). Additionally, the medial lamina is just a short flange that does not overhang the inner margin of the endomerite in *S. columbianus*, whereas it is much longer and extends into a basal lobe that does overhang this margin in *S. piger*. In nonsexual features, the tubercles are much stronger and more clearly demarcated from each other in *S. columbianus*; they are smaller, more lowly rounded, and tend to merge with one another in *S. piger*. Similarly, the paranotal margins are much more deeply indented and emarginate in *S. columbianus*, in contrast to the nearly smooth condition in *S. piger*.

### *Scytonotus columbianus* Chamberlin

Figs. 7–8

*Scytonotus columbianus* Chamberlin, 1920:166–167, fig. 16. Attems, 1940:158. Chamberlin and Hoffman, 1958:72. Kevan, 1983:2969. Shelley, 1990:20.

*Type specimens*—Male holotype (MCZ) taken by J. B. Tyrrell, 26 September 1883, in the Columbia Valley (probably the valley of the Columbia River), British Columbia, Canada. One male and one female paratypes (MCZ) taken by same collector, 1 September 1883, from a “swamp, tobacco plain” in the same locality.

*Diagnosis*—Tibiae of legs 13–20/22 in males without distal lobes; endomerite much shorter than tibiotarsus, segregated from the

latter for most of length; medial lamina a short, inconspicuous, broadly rounded flange at level of pulvillus, not overhanging inner margin of endomerite; distal lamina with widely separated, poorly demarcated, subacuminate teeth, proximal one larger; lateral lamina moderately broad, overhanging inner margin of endomerite (Figs. 7–8); females with paranota of segments 5–9 not reduced.

*Variation*—The flange-like medial lamina is narrower and barely detectable on the male from Yoho National Park, and the proximal tooth on the distal lamina is much larger than the apical tooth in this individual.

*Ecology*—The specimens that I collected in Mt. Revelstoke and Kootenay National Parks, British Columbia, were encountered under wet deciduous litter near streams. The male from Washington was recovered from a pitfall trap in an old field.

*Distribution*—Extending from the Selkirk and Rocky Mountains at Revelstoke and Yoho National Parks, British Columbia, to the northeastern corner of Washington, ranging westward into the Columbia River Valley (Fig. 10). Specimens were examined as follows:

CANADA: BRITISH COLUMBIA: *Mt. Revelstoke Nat. Pk.*, Skunk Cabbage area, 2 juvs., 9 August 1989, R. M. Shelley (NCSM). *Yoho Nat. Pk.*, 2 mi (3.2 km) S Takkakaw Falls, M, 5 October 1963, A. Nimmo (VMNH) and Kicking Horse Camp, F, 5 October 1963, D. R. Whitehead (VMNH). *10 mi (16 km) E Golden*, F, 2 juvs., 28 June 1988, S. & J. Peck (NCSM). *Kootenay Nat. Pk.*, trail to Cobb Cpgd., juv., 7 August 1989, R. M. Shelley (NCSM). *Columbia Valley*, site not specified, 2M, F, 1 and 26 September 1883, J. B. Tyrrell (MCZ) TYPE LOCALITY. *Kaslo*, F, 18 juvs., 30 June–4 July 1903, A. M. Caudell (NMNH). *16 km E. Salmo*, along Hwy. 3, ca. 1 mi (1.6 km) E jct. Hwy. 6, 2 juvs., 6 August 1989, R. M. Shelley (NCSM).

USA: WASHINGTON: *Pend Oreille Co.*, ca. 7 mi (11.2 km) S Usk, Deer Cr., along WA hwy. 211 just S Davis L., 48.210°N, 117.289°W, 6M, F, 29 August–9 September 1980, R. Crawford (UWBM).

### The *Bergrothi* Group

Aside from the allopatric population of *S. insulanus* in eastern Washington, the *bergrothi* group is found exclusively along the Pacific Ocean. It is the only lineage occurring west of the Cascades, and *S. bergrothi* extends across the crest and onto the eastern slope of these mountains in Yakima and Kittitas counties, Washington. Anatomically, the endomerites are longer than the tibiotarsi because the distal lamina is prolonged to varying degrees. The latter



also bends sharply or curves so that it is angular with respect to the endomerite stem, and it is divided in *S. insulanus*. The medial laminae exhibit a distal tooth in *S. bergrothi* and *simplex*, and the lateral laminae are short with rounded lobes except on *S. simplex*, which possesses a lightly serrate basal lobe and a distal tooth. *Scytonotus bergrothi* and *insulanus* are broadly sympatric in coastal Washington, northwestern Oregon, and southwestern British Columbia, whereas *S. simplex* is parapatric to the south, with only minimal overlap of *S. bergrothi* (Figs. 20, 32). I am unable to resolve the relationships among the components and show them in Figure 34 as an unresolved trichotomy.

*Components*—*bergrothi* Chamberlin, *insulanus* Attems, *simplex* Chamberlin.

### *Scytonotus insulanus* Attems

Figs. 11–12

*Scytonotus insulanus* Attems, 1931:147–149, figs. 240–245; 1940:157–158, figs. 229–231. Chamberlin and Hoffman, 1958:73. Kevan, 1983:2969.

*Scytonotus insulans*: Shelley, 1990:20.

*Type specimens*—One male and one female syntypes (NMV) taken by an unknown collector on an unspecified date in 1934 at Nanaimo, Vancouver Island, British Columbia, Canada.

*Diagnosis*—Tibiae of legs 13–22 in males with distal lobes; endomerite much longer than tibiotarsus; medial lamina relatively short, with moderately acuminate flange overhanging inner margin of endomerite; distal lamina apically divided, medial branch slightly expanded and broadly rounded basally, tapering into greatly prolonged, strongly decurved projection, tip narrowly rounded, lateral branch about 1/3 as long as latter, expanding distad and tapering slightly to subacuminate tip; lateral lamina expanding into moderate-size, narrowly rounded lobe, overhanging inner margin of endomerite (Figs. 11–12); paranota of segments 5–9 reduced in females.

*Variation*—There is very little variation among the gonopods of *S. insulanus*. In the male from 12 mi (19.2 km) east of Salem, Marion County, Oregon, the flange on the medial lamina is narrower and more rounded than that of the type, and the lobe on the lateral lamina is smaller, more pointed, and located more proximad. A few other individuals exhibit similar, minor variation in the size of these structures, but most gonopods agree closely with the type.

*Ecology*—Labels with preserved samples give the following microhabitat information for *S. insulanus*: alder and birch litter,

moss, maple and dogwood duff, hemlock duff, beach grass debris, and dried seaweed.

*Distribution*—Along the Pacific Coast from Yakutat Bay, Alaska, to eastern Douglas County, Oregon, with an allopatric population in southeastern Washington, around 308 mi (493 km) from the closest locality (Figs. 10, 19–20). Because *S. insulanus* is the only species represented by males in Alaska and Canada north of Vancouver Island, it is assigned to juvenile and female only samples from this area. Specimens were examined as follows:

CANADA: BRITISH COLUMBIA: VANCOUVER ISLAND: *Nanaimo*, M, F, 1934, collector unknown (NMV) and 4M, 2F, 17 October 1907, R. Paessler (ZMH) TYPE LOCALITY.

MAINLAND SITES: *Stewart*, 5 juvs., 7 August 1988, S. & J. Peck (NCSM). *Terrace*, 4 juvs., 10 August 1988, S. & J. Peck (NCSM). *Vancouver*, 2M, 2F, 22 February and 4 April 1933, H. B. Leach (NMNH).

USA: ALASKA: *Juneau*, M, 3F, 28 April 1945, J. C. Chamberlin (NMNH). *Baranof I.*, Sitka, juv., June 1899, Harriman Exp. (NMNH). *Kupreanof I.*, Lindenberg Penin., Ohmers Slough, M, 29 August 1951 (NMNH). *Mitkof I.*, 8 mi (12.8 km) N Ideal Cove, M, 3 September 1951, B. Malkin (NMNH). *Wrangell I.*, Wrangell, 2M, 1951, B. Malkin (NMNH). *Etolin I.*, Menefee Inlet, M, 21 September 1951, B. Malkin (NMNH).

WASHINGTON: *Whatcom Co.*, Custer, 2M, 3 April 1951, J. T. Davis (UWBM). *Skagit Co.*, Chuckanut Dr., S of Bow, 48.513°N 122.374°W, 12M 5F, 30 March 1982, R. Crawford (UWBM); and Pipeline Rd. at WA hwy 20 nr. Lyman, 48.527°N, 122.056°W, 2M, 28 September 1975, R. Crawford (UWBM). *Snohomish Co.*, Mukilteo, 2M, 12 February 1905, R. Paessler (ZMH). *Clallam Co.*, Olympic Nat. Pk., Waterhole Camp, 47.94°N, 123.42°W, 2M, 30 August 1966, R. Crawford (UWBM). *Grays Harbor Co.*, Westport, 3M, 8F, date unknown, J. Wilcox (NMNH); and Pacific Beach, 2 juvs., 14 May 1933, R. V. Chamberlin (FSCA). *Thurston Co.*, Nisqually R. Delta, 47.075°N, 122.707°W, M, 23 October 1984, R. Crawford (UWBM). *Pacific Co.*, Cape Shoalwater, 5M, 10F, 18 February 1987, R. Crawford (UWBM). *Wahkiakum Co.*, Grays River, Swede Park, 46.356°N, 123.58°N, M, F, 24 October 1984, R. Crawford (UWBM). *Whitman Co.*, 4 mi (6.4 km) N Colfax, juv., 30 May 1941, J. C. Chamberlin (NMNH); and 8 mi (12.8 km) SW Pullman, Lyle Grove, M, F, 3 March 1973, W. J. Turner (WSU).



OREGON: *Clatsop Co.*, Fort Stevens St. Pk., M, 27 November 1971, E. M. Benedict (WAS). *Columbia Co.*, 3 mi (4.8 km) SW Clatskanie, 2M, F, 8 January 1972, E. M. Benedict (WAS). *Multnomah Co.*, Portland, 250 NE 114 Ave., M, FF, juvs., 9 April 1957, D. B. Monroe (FSCA), and Macleay Park, 3F, 2 January 1970, J. S. Buckett (UCD). *Washington Co.*, 1.1 mi (1.8 km) N Gaston, along OR hwy 47, M, 2 October 1971, E. M. Benedict (WAS). *Yamhill Co.*, 5 mi (8 km) NE Newberg, M, 26 October 1968, K. Goeden (UCD); and 0.2 mi (0.3 km) S Wapata, 4M, 2 October 1971, E. M. Benedict (WAS). *Clackamas Co.*, 1.9 mi (3.0 km) W Carver, MM, FF, 9 October 1971, E. M. Benedict (WAS); and 2 mi (3.2 km) E. Rhododendron, 2 juvs., 18 November 1969, K. Goeden (UCD). *Marion Co.*, 18 mi (28.8 km) N Salem, juvs., date and collector unknown (NMNH); 12 mi (19.2 km) NE Salem, M, 15 October 1968, B. Brown (UCD); Salem, F, 29 January 1921, C. D. Duncan (NMNH); 2.5 mi (4.0 km) NW Mehama, 3M, 2F, 1 March 1969, E. M. Fisher (UCD) and MM, FF, 24 February 1970, J. S. Buckett, M. R. Gardner (UCD); 1.5 mi (2.4 km) S Mill City, F, 9 March 1969, E. M. Fisher (UCD); and 1 mi (1.6 km) E Gates, 2F, 9 March 1969, E. M. Fisher (UCD). *Jefferson Co.*, Spring Creek, exact location unknown, M, 19 April 1952, V. Roth (FSCA). *Benton Co.*, 6 mi (9.6 km) N Corvallis, Peavy Arboretum, F, 17 January 1973, L. Russell (VMNH); 5 mi (8 km) N Corvallis, Sulphur Spgs., 3 juvs., 26 March 1969, E. M. Fisher (UCD); Oak Cr., M, F, 18 February 1972, L. Russell (VNMH); and McDonald For., ca. 5 mi (8 km) NNW Corvallis, M, F, 20 September 1959, V. Roth (AMNH), 3M, F, 31 October 1968, 2F, 18 December 1968, and MM, FF, 26 February 1969, R. L. Westcott (UCD), and 3F, 4 March 1969, E. M. Fisher (UCD); and Corvallis, juvs., 1896, A. B. Cordley (NMNH), F, 27 January 1936, G. Ferguson (NMNH), and juv., 13 June 1949, R. D. Walters (NMNH). *Lane Co.* McCredie Spgs., 3M, 6F, 7 October 1947, B. Malkin (NMNH); 6 mi (9.6 km) S Oakridge, M, 4F, 4 March 1972, E. M. Benedict (WAS); and Dolly Varden Cpgd., along OR hwy 58 E of Oakridge, 7M, 4F, 4 March 1972, E. M. Benedict (WAS). *Douglas Co.*, 3 mi (4.8 km) S, 9 mi (14.4 km) E Steamboat, Eagle Rock Cpgd. along OR hwy 138, 2M, 4F, 30 October 1971, E. M. Benedict (WAS); 3 mi (4.8 km) S, 10 mi (16 km) E Steamboat, Boulder Flat Cpgd. along OR hwy. 138, M, 30 October 1971, E. M. Benedict (WAS); and 5 mi (8 km) S, 1 mi (1.6 km) E Steamboat, Island Cpgd. along OR hwy. 138, 4M, 3F, 30 October 1971, E. M. Benedict (WAS).

The following literature records of *Scytonotus* sp. are considered referable to *S. insulanus*.

USA: ALASKA: *Yakutat Bay* (Cook 1904).

WASHINGTON: *Clallam Co.*, *Elwha* (Causey 1954b).

*Remarks*—The records from the Columbia Plateau Physiographic Province in Whitman County, Washington, are quite surprising, but the data appear accurate, and the adults conform to all the diagnostic traits of *S. insulanus*. This is the only record of the genus from southeastern Washington, and it suggests occurrence of *S. insulanus* in the Hell's Canyon area of northeastern Oregon. The Lane and Douglas county Oregon sites, about 90 mi (144 km) from the closest locality, in Benton County, also may represent an allopatric population.

*Scytonotus bergrothi* Chamberlin

Figs. 13–14

*Scytonotus* sp. Cook, 1904:pl. 4, figs. 2a–d.

*Scytonotus bergrothi* Chamberlin, 1911:262–264, fig. 16. Attems, 1940:158. Chamberlin and Hoffman, 1958:72. Kevan, 1983:2969.

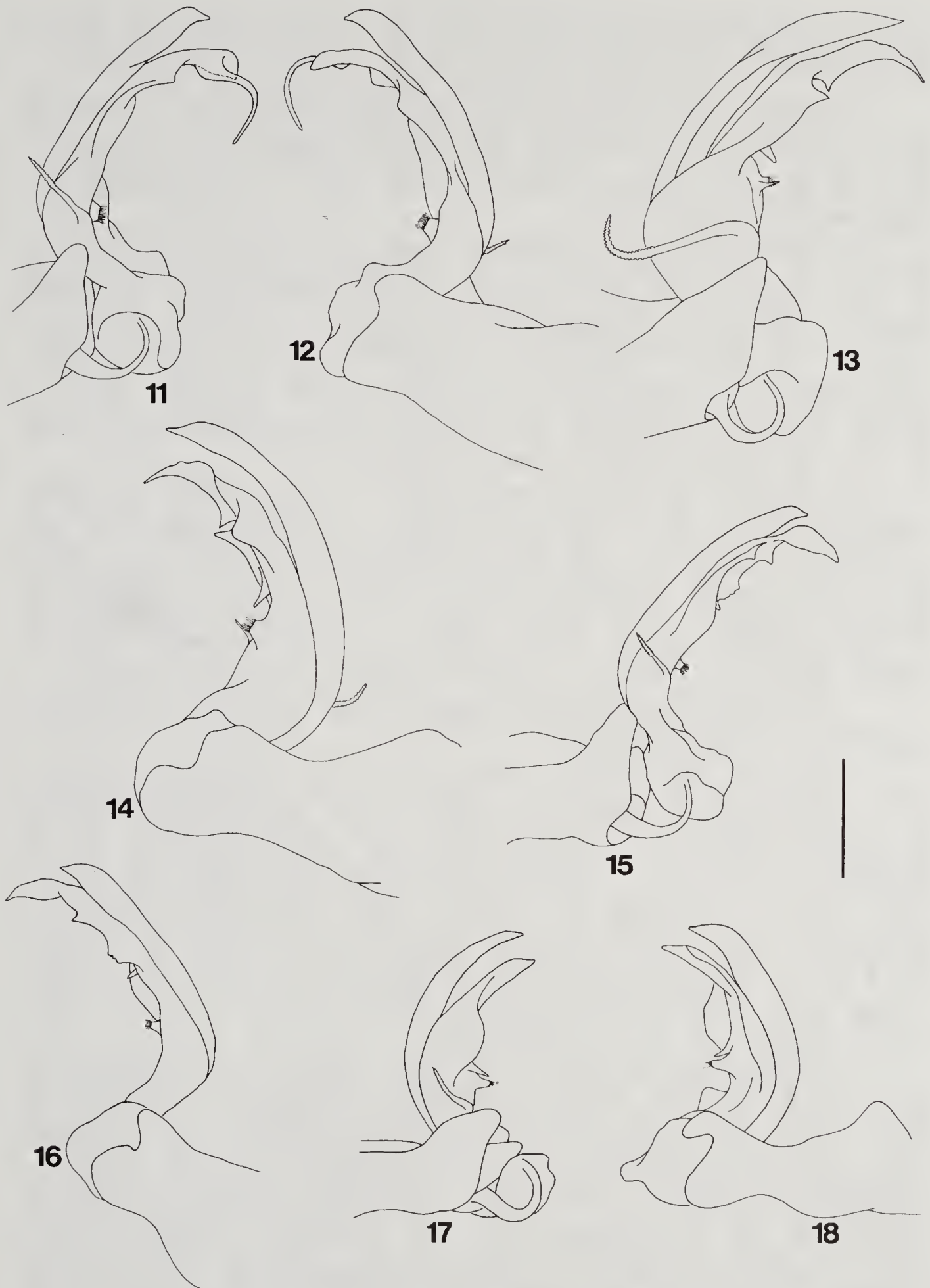
*Scytonotus pallidus* Attems, 1931:145–147, figs. 234–239; 1940:156–157, figs. 227–228. Causey, 1954:82. Shelley, 1990:20.

*Type specimens*—One male and 3 female syntypes (NMNH) collected by D. E. Bergroth on an unknown date at Bremerton, Kitsap County, Washington.

*Diagnosis*—Tibiae of legs 13–21 in males with distal lobes; endomerite slightly longer than tibiotarsus; medial lamina expanding into broad flange for most of length, terminating in sharply acute distal tooth; distal lamina with smaller, sharply acute tooth proximad, narrowing, curving gently, and slightly prolonged thereafter, apically acuminate, with or without variable undulations, short teeth, or spurs on outer margin; lateral lamina relatively short, expanding into moderately large, broadly rounded lobe, overhanging inner margin of endomerite (Figs. 13–14); paranota of segments 5–9 reduced in females.

*Variation*—The most notable gonopodal variation are the enlargements of the undulations on the outer margin of the distal lamina in males from British Columbia. Barely noticeable in southern specimens, the undulations become larger and more distinct around Vancouver and on Vancouver Island, and even are denticulate on a few males. Other gonopodal variation involves minor differences in the length and position of the spur on the inner margin of the endomerite near the hairpad. It projects well beyond the hairpad and is visible in lateral view in some males but is shorter in others; it can also be distal or proximal to the pulvillus. The relative sizes of the distal tooth on the medial lamina and the basal tooth





Figs. 11-18. 11-12, *S. insulanus*. 11, left gonopod of male syntype, medial view. 12, the same, lateral view. 13-14, *S. bergrothi*. 13, left gonopod of male from Jefferson County, Washington, medial view. 14, the same, lateral view. 15-16, *S. simplex*. 15, left gonopod of male from Lincoln County, Oregon, medial view. 16, the same, lateral view. 17-18, *S. inornatus*. 17, left gonopod of holotype, medial view. 18, the same, lateral view. Scale line = 0.5 mm for all figures.

on the distal lamina also vary, and the flange below the former and the lobe on the lateral lamina are narrower on some males.

*Ecology*—Labels with preserved samples indicate that *S. bergrothi* was taken from the following microhabitats: alder litter, under wet bark of decaying logs by ponds, under bark of Douglas-firs, and moss on tree trunks.

*Distribution*—Known definitely from southern Vancouver Island and the mainland of southwestern British Columbia to the northwestern corner of Oregon, with an allopatric population some 151 mi (251 km) to the south in the northeastern corner of Lane County. The range also extends across the crest of the Cascades onto the eastern foothills in Kittitas and Yakima counties, Washington (Figs. 19–20). Specimens were examined as follows:

CANADA: BRITISH COLUMBIA: VANCOUVER ISLAND: *Parksville*, 10 juvs., 17 September 1935, R. V. Chamberlin, W. Ivie (NMNH). *Cameron L.*, 2M, 15 September 1935, R. V. Chamberlin, W. Ivie (NMNH). *Errington*, 2M, 1 October 1951, collector unknown (NMNH). *Sooke*, Sooke Harbor, M, 9 February 1969, E. Thorn (RBCM). *Victoria*, 2M, 1949, collector unknown (RBCM).

OTHER ISLANDS: *S. Pender I.*, M, 2 juvs., 1 September 1955, G. C. Carl (NMNH).

MAINLAND SITES: *Powell L.*, M, 20 September 1938, R. H. Boyd (NMNH). *Vancouver*, MM, FF, 20 August 1932, 22 and 26 March 1933, and 3 April 1937, H. B. Leach (NMNH); 4M, 14 September 1935, R. V. Chamberlin, W. Ivie (NMNH); 5M, 3F, 2 juvs., 1938, G. J. Spencer (NMNH); and Univ. of BC, M, F, 3 November 1960, D. G. Bandoni (UBC). *Mt. Seymour*, F, 31 May 1931, H. B. Leach (NMNH). *North Surrey*, 11M, 20 juvs., 6 September 1965, J. & W. Ivie (AMNH).

USA: WASHINGTON: *San Juan Co.*, San Juan Islands, 4 juvs., 1938, collector unknown (NMNH). *Whatcom Co.*, Bellingham, *Yew St.*, M, 4 October 1988, R. Crawford (UWBM); and *Chuckanut Mt.*, 48.671°N, 122.471°W, 2M, 1 September 1975, R. Crawford (UWBM). *Skagit Co.*, *Samish R.*, NW Sedro Woolley, 48.552°N, 122.295°W, M, 8 September 1977, R. Crawford (UWBM); *Island Co.*, *Deception Pass St. Pk.*, 5 juvs., 21 August 1990, R. M. Shelley (NCSM); 7.5 mi (12.0 km) NNE Oak Harbor, 3 March 1988, Wright, Nelly (NCSM); 2 mi (3.2 km) E Ebey's Landing, Whidbey, 48.188°N, 122.70°W, M, F, 4 December 1988, R. Crawford (UWBM); and *S. Whidby St. Pk.*, 5 juvs., 21 August 1990, R. M. Shelley (NCSM). *Mason Co.*, 11 mi (17.6 km) S Goose Prairie, 3M, 10 February 1991, K. Dorweiler (UWBM); and *S of Hamma Hamma R.*, along US hwy 101, NW Eldon, 47.56°N, 123.072°W,



M, 2F, 15 October 1977, R. Crawford (UWBM). *Jefferson Co.*, 5.5 mi (8.8 km) S Brinnon, along US Hwy. 101, 2M, 23 September 1978, A. K. Johnson (NCSM); and Ft. Flagler St. Pk., M, 19 August 1975, S. Lefler (UWBM). *Grays Harbor Co.*, Canyon R., ca. 7 mi (11.2 km) WNW Matlock, 47.262°N, 123.526°W, 8M, F, 29 August-18 October 1976, R. Crawford (UWBM); and Chehalis R. nr. Porter, 46.93°N, 123.31°W, M, 24 December 1920, R. H. Palmer (UWBM). *Kitsap Co.*, Bremerton, M, 3F, date unknown, D. E. Bergroth (NMNH) TYPE LOCALITY. *Snohomish Co.*, Marysville, juv., 10 August 1929, R. V. Chamberlin (NMNH); Mukilteo, M, F, 1934, collector unknown (NMV, ZMH); L. Ballinger, nr. King Co. line, 47.77°N, 122.32°W, 2M, F, 10 November 1939, E. F. Dailey (UWBM); L. Stevens, 47.99°N, 122.07°W, M, F, 16 November 1921, V. G. Wood (UWBM); and Skykomish R., nr. Gold Bar on US hwy. 2, 47.837°N, 121.657°W, M, 25 October 1980, R. E. Nelson (UWBM). *King Co.*, Seattle, U.WA campus, 2M, 7F, 8 January 1932 and 21 November 1940, E. F. Dailey (UWBM); Seattle, 2F, 9 April 1936, M. H. Hatch (UWBM), 2M, 2F, 9 April 1936, collector unknown (FSCA), 3M, 4F, 22 October 1941, E. I. Smith (VMNH), M, 28 September 1944, H. S. Dybas (FMNH), and Discovery Park, 8M, 5F, 19 October 1980, R. Crawford (UWBM); Rutherford Slough nr. Fall City, 47.575°N, 121.888°W, 2M, 2F, 1 November 1980, R. E. Nelson (UWBM); 1 mi (1.6 km) E North Bend, M, 3 May 1983, W. F. Barr (NCSM); North Bend, M, F, 27 April 1939, E. F. Dailey (UWBM); Newcastle Hills, M, 6 April 1985, R. Crawford (UWBM); Snoqualmie Falls, 5 juvs., 16 September 1935, R. V. Chamberlin, W. Ivie (NMNH); Snoqualmie Pass, 2 juvs., 11 August 1929, R. V. Chamberlin (NMNH) and F, 16 September 1935, R. V. Chamberlin, W. Ivie (NMNH); and Bridle Trails St. Pk., M, 2F, 16 March 1985, R. Crawford (UWBM). *Pierce Co.*, Mount Rainier Nat. Pk., locality not specified, 2M, F, 4 juvs., 12 September 1965, J. & W. Ivie (AMNH), Paradise Valley, F, juv., July 1922, Jones (NMNH), 2M, 2F, 28 August 1946 and 1 August 1948, E. F. Dailey (UWBM), nr. Paradise Lodge, 4 juvs., 30 June 1980, M. A. Brittain (NCSM), Tipsoo Lake, F, 5 July 1938, W. Ivie (NMNH), and Tahoma Cr., 5M, 7F, 13 juvs., 14 August 1947, E. F. Dailey (UWBM); Horseshoe L., nr. Eatonville, 46.915°N, 122.271°W, M, 9 juvs., 4 September 1977, A. Ruggles (UWBM); and Ft. Lewis, F, 5 January 1946, P. H. Arnaud (NMNH). *Thurston Co.*, Olympia, M, F, 24 March 1932, T. Kincaid (UWBM) and 2M, 7 juvs., 28 August 1959, W. J. Gertsch (AMNH). *Lewis Co.*, 2.5 mi (4.0 km) S Packwood, Johnson Cr. Rd., 2M, juvs., 22 September 1978, A. K. Johnson (NCSM); and Lewis and Clark St. Pk., M, 29 October 1988, R.

Crawford (UWBM). *Kittitas Co.*, Cle Elum, juv., 7 May 1933, W. W. Baker (NMNH). *Yakima Co.*, White Swan, 6 juvs., 7 May 1933, W. W. Baker (NMNH).

OREGON: *Clatsop Co.*, Youngs R. Falls Pk., nr. Olney, F, 4 June 1991, R. M. Shelley (NCSM); and 3 mi (4.8 km) SE Olney, M, 27 November 1971, E. M. Benedict (WAS). *Lane Co.*, 22 mi (35.2 km) NE McKenzie Bridge, M, F, 16 October 1971, E. M. Benedict (WAS).

The following literature record to *Scytonotus* sp. is considered referable to *S. bergrothi*:

USA: WASHINGTON: *Island Co.*, Sunnyside (Causey 1954b).

*Remarks*—The long, barbed, acicular projection on the medial face of the endomerite curves ventrad distally in all males that I examined. Its length and curvature seem to be unique to, and possibly diagnostic of, *S. bergrothi*, as the structure is much shorter and at most only slightly curved in males of the other western species.

As stated on the vial label and reported by Attems (1931), the type locality of *S. pallidus*, a synonym of *S. bergrothi*, is Mukilteo, Snohomish County, Washington, and not Vancouver Island, British Columbia, as reported by Chamberlin and Hoffman (1958). Attems (1931, 1940) confusingly records Nanaimo, Vancouver Island, under *S. pallidus* but states in the prior work that this is the locality of *S. insulanus*. I have not seen any males of *S. bergrothi* from Nanaimo, but Parksville and Errington are very near, and *S. bergrothi* as well as *S. insulanus* should be expected at Nanaimo.

*Scytonotus insulanus* and *S. bergrothi* occur sympatrically from southwestern British Columbia to just south of the Columbia River in Clatsop County, Oregon, although the latter is much more abundant in Washington. South of the Columbia River, only *S. insulanus* has been taken in the Coast Range and Willamette Valley of Oregon to about the level of Corvallis, where it overlaps slightly the northern periphery of *S. simplex* (Figs. 19–20, 31). The species, therefore, tend to replace each other in western Oregon and Washington, and as stated previously only *S. insulanus* is known definitely from northern British Columbia and Alaska. Neither species has been encountered on the Queen Charlotte Islands, nor have unidentifiable juveniles been taken there. As this archipelago has been intensively sampled by arthropod biologists for many years, it seems that *Scytonotus* does not occur there.



*Scytonotus simplex* Chamberlin

Figs. 15–16

*Scytonotus simplex* Chamberlin, 1941:16, pl. 3, fig. 30. Chamberlin and Hoffman, 1958:73. Kevan, 1983:2969.

*Type specimens*—Male holotype, female allotype, and one male and one female paratypes (NMNH) collected by J. C. Chamberlin, 18 November 1939, at Days Creek, Douglas County, Oregon.

*Diagnosis*—Tibiae of legs 13–20 in males with distal lobes; endomerite moderately longer than tibiotarsus; medial lamina expanding into moderate-size flange for proximal 2/3 of length, indenting broadly, then expanding into moderate-size, acuminate, distal tooth; distal lamina bent nearly perpendicular to tibiotarsus, narrowly expanded basally, inner margin curving slightly bisinuate into subacuminate tip; lateral lamina located well distal to pulvillus, expanding into moderate-size basal lobe with lightly irregular margin, narrowing slightly, then expanding into sharply acute tooth distal to mid-length (Figs. 15–16); paranota of segments 5–9 reduced in females.

*Variation*—The distal lamina and the distal parts of the medial and lateral laminae are closely similar on all specimens, but the proximal parts of the last two lamellae vary considerably. The breadth of the basal flange on the medial lamina is often narrower than in the illustrated male, and an individual from Del Norte County, California, has a sharply acute tooth at the corner of the flange. The distal tooth on the medial lamina is also much larger in the male from San Joaquin County, California. On the lateral lamina, the basal serrated lobe varies considerably. In a male from Coos County, Oregon, it is longer and located more proximad; it is also longer and narrower in individuals from Trinity County, California. Conversely, it is much shorter and narrower in the San Joaquin County male and is barely detectable in one from Del Norte County.

*Ecology*—Labels with preserved samples indicate the following microhabitats for *S. simplex*: pine tree trunks after rain, hemlock duff, birch litter, and under wet leaves.

*Distribution*—Along the Pacific Coast from northern Lincoln County, Oregon, to San Francisco Bay and the northern San Joaquin Valley, California (Fig. 20). The range extends eastward onto the western slope of the Cascades in Lane, Douglas, and Jackson counties, Oregon, and overlaps slightly both the main area and the Lane County population of *S. insulanus* (Fig. 31). Specimens were examined as follows:

OREGON: *Lincoln Co.*, 0.6 mi (0.9 km) NW Elk City, along Yaquina R., M, F, 20 December 1971, E. M. Benedict (WAS). 5.5 mi (8.8 km) E, 2.5 mi (4.0 km) S, Tidewater, along Alsea R., 3M,



Figs. 19–20. Distributions of *Scytonotus* spp. along the Pacific Coast of North America. **19**, distributions in Alaska and British Columbia. **20**, distributions in western Washington, Oregon, and California. Solid stars, *S. insulanus*; dots, *S. bergrothi*; squares, *S. simplex*; star in dot, *S. inornatus*; open stars, literature records of *S. insulanus* considered reliable; question marks, female or juvenile samples and literature records that could be either *S. insulanus* or *bergrothi*.



3 juvs., 14 September 1977, A. K. Johnson (NCSM); and 10 mi (16 km) SE Kernville, M, 9F, 17 February 1969, R. L. Westcott, J. S. Buckett (UCD); Saddleback Mtn., 2 juvs., 12 August 1959, J. C. Dirks-Edmonds (NMNH); between Tidewater and Waldport, juvs., 25 April 1937, M, 2F, 19 September 1946, J. C. Chamberlin (FSCA, NMNH). *Tillamook Co.*, Boyer, juv., date and collector unknown (NMNH). *Benton Co.*, 2.3 mi (3.7 km) NW Glenbrook, S. Fk. Alsea R., 2M, 8F, 4 December 1971, E. M. Benedict (WAS); and 0.5 mi (0.8 km) NW Glenbrook, S. Fk. Alsea R., F, 4 December 1971, E. M. Benedict (WAS). *Lane Co.*, October 1927, and M, 1 November 1927, D. T. Jones (NMNH); 11 mi (17.6 km) W Eugene, 5M, F, 4 December 1971, E. M. Benedict (WAS); and Dexter, M, January 1970, J. S. Buckett (UCD). *Douglas Co.*, 20 mi (32 km) E Reedsport, along Vincent Cr., 4M, F, 4 October 1968, J. Schuh (FSCA); 11 mi (17.6 km) E, 4 mi (6.4 km) S Alleghany, Millicoma Tree Farm, M, F, 21 November 1971, E. M. Benedict (WAS); 8 mi (12.8 km) W Scottsburg, juvs., 6 September 1970, M. R. Gardner, T. L. Slay (UCD); 7 mi (11.2 km) W Scottsburg, along Umpqua R., M, 11 December 1971, E. M. Benedict (WAS); 3.2 mi (5.1 km) NE Scottsburg, 6M, F, 11 December 1971, E. M. Benedict (WAS); 9 mi (14.4 km) SW Cottage Grove, juvs., 23 August 1959, W. J. Gertsch, V. Roth (NMNH); 6 mi (9.6 km) S Cottage Grove, Divide, F, 28 April 1937, J. C. Chamberlin (NMNH); 8 mi (12.8 km) and 20 mi (32 km) NE Sutherlin, 2F, 13 March 1968, J. S. Buckett, M. R. Gardner (UCD); Tree Horn Cpgd., along OR hwy. 138 E of Steamboat, F, 10 June 1991, R. M. Shelley (NCSM); 4.5 mi (7.2 km) E Wells Cr. Ranger Sta., M, 11 December 1971, E. M. Benedict (WAS); nr. Roseburg, M, F, 30 September 1931, collector unknown (NMNH); Days Creek, 2M, 2F, 18 November 1939, J. C. Chamberlin (NMNH) TYPE LOCALITY; and 1 mi (1.6 km) S, 2 mi (3.2 km) W Ash, 6M, 9F, 11 December 1971, E. M. Benedict (WAS). *Coos Co.*, 2.5 mi (4.0 km) E Bandon, along OR hwy. 425, 2M, F, 24 September 1978, A. K. Johnson (NCSM); 0.25 mi (0.4 km) N Boundary, M, 19 February 1972, E. M. Benedict (WAS); Myrtle Grove Cpgd., MM, FF, 13 February 1972, E. M. Benedict (WAS); and Charleston, juvs., 15 August 1947, I. Newell (NMNH). *Jackson Co.*, Applegate, juvs., 20 August 1977, R. O. Schuster (UCD); and Ashland, juvs., 9 July 1929 and 29 August 1931, R. V. Chamberlin, W. Ivie (NMNH). *Josephine Co.*, Oregon Caves Nat. Mon., 2F, 11 June 1991, R. M. Shelley (NCSM); and 1 mi (1.6 km) S O'Brien, M, 18 December 1971, E. M. Benedict (WAS). *Curry Co.*, Port Orford, M, 19 August 1961, W. Suter (FSCA); Humbug Mtn., ca. 5 mi (8 km) S Port Orford, 7 juvs., 19

August 1961, W. Suter (FSCA); Pistol River, juvs., 7 July 1951, B. Malkin (NMNH); 4 mi (6.4 km) S Pistol R., along US hwy 101, MM, FF, 12 February 1972, E. M. Benedict (WAS); and 2 mi (3.2 km) N Brookings, M, 31 September 1959, V. Roth (AMNH).

CALIFORNIA: *Del Norte Co.*, 7 mi (11.2 km) ENE Gasquet, Patrick Cr. Cpgd., M, F, 21–22 December 1979, A. K. Johnson (NCSM); 5 mi (8 km) S Crescent City, juv., 8 September 1958, L. M. Smith (VMNH); and 6 mi (9.6 km) N. Klamath, juvs., 13 August 1953, G. A. Marsh, R. O. Schuster (UCD). *Humboldt Co.*, 1.5 mi (2.4 km) NE Orick, Redwood Nat. Pk., Redwood Cr., M, 2F, 26 March 1977, A. K. Johnson (NCSM) and 2F, 1 June 1991, R. W. Baumann, Stark (BYU), along Panther Cr., 2M, F, 29 August 1981, A. K. Johnson (NCSM) and MM, FF, 29–30 August 1981, D. G. Anderson (RNP), along Wolfe Cr., MM, FF, 27–28 September 1981, D. G. Anderson (RNP), and along Tom McDonald Cr., MM, FF, 11–12 September 1981, D. G. Anderson (RNP); Fickel Hill Rd., 3M, 18 September 1976, A. K. Johnson (NCSM); Big Lagoon, 2M, 2F, 13 August 1953, G. A. Marsh, R. O. Schuster (NMNH) and F, 12 November 1974, A. K. Johnson (NCSM); Patrick Pt. St. Pk., M, 21 September 1964, J. & W. Ivie (AMNH); Trinidad, M, 16 July 1968, W. Ivie (AMNH); 2 mi (3.2 km) E Trinidad, 20 January 1976, A. K. Johnson (NCSM); 2 mi (3.2 km) S Hoopa, F, 29 June 1991, R. M. Shelley (NCSM); 14 mi (22.4 km) W Willow Cr., 4 juvs., 21 August 1959, W. J. Gertsch, V. Roth (NMNH); Jolly Giant Cyn. nr. Arcata, 2M, 23 November 1974, A. K. Johnson (NCSM); Arcata, 12 juvs., 23 July 1969, C. Slobodchikoff (CIS); Eureka, juvs., date unknown, H. S. Barber (NMNH) and 3 juvs., 13 July 1937, R. V. Chamberlin (NMNH); and Dyersville, juvs., date unknown, G. A. Marsh, R. O. Schuster (NMNH). *Trinity Co.*, 1.5 mi (2.4 km) E Hawkin's Bar, along CA hwy 229, 11M, F, 9 October 1976, A. K. Johnson (NCSM). *Mendocino Co.*, 2.5 mi (4.0 km) N Mendocino, juvs., 30 June 1964, J. S. Buckett, M. R. Gardner (UCD); and Mendocino, juvs., 6 March 1957, J. R. Helfer, R. O. Schuster (NMNH) and M, 11 December 1969, J. R. Helfer (UCD). *Sonoma Co.*, 1 mi (1.6 km) SE Bodega Bay, 3M, 3F, 5 October 1963, P. Rubtzoff (FSCA); Sebastopol, 5 juvs., 25 August 1957, R. E. Darby (NMNH) and 2F, date and collector unknown (BMNH); and ca. 6 mi (9.6 km) NE Santa Rosa, Petrified For., juvs., 26 August 1931, W. Ivie (NMNH). *Marin Co.*, Lagunitas, 2M, 9 January 1965, J. S. Buckett, M. R. Gardner (UCD); 2 mi (3.2 km) N Bolinas, 6M, F, 22 September 1963, J. and W. Ivie (AMNH); Bolinas Jct., 21M, 2 juvs., 21 September 1965, W. Ivie (AMNH); Mill Valley, F, date and collector unknown (BMNH); 2 mi (3.2



km) W Inverness, 2F, 1 May 1976, J. T. Doyen (CIS); and Inverness Ridge, M, 17 November 1962, N. B. Causey (FSCA) and MM, FF, 9 October 1963, J. S. Bucket (UCD, FSCA). *San Joaquin Co.*, Stockton, M, 27 October 1973, L. S. Hawkins (NCSM).

*Remarks*—The name of this species is puzzling and clearly a misnomer; the gonopod of *S. simplex* is hardly “simple” either alone or in comparison with those of the other species that had been proposed by 1941. One wonders about Chamberlin’s reasoning, because the only species with truly “simple” gonopods is *S. inornatus*.

#### The *Inornatus* Group

A monobasic lineage, this group is characterized by an absence of modifications that is most noticeable on the distal lamina. The medial lamina expands into a broad flange; the lateral lamina is long and slender; and the endomerite and tibiotarsus are subequal in length. The lineage is thus the most plesiomorphic in *Scytonotus*, and from its apparently restricted distribution, the lone component species appears to be a relict and the sole surviving remnant of its line. Such a nondescript, unmodified ancestral form could have given rise to both other lineages, and its occurrence on the eastern slope of the Cascades points to this general region as the likely source for the other lines and the primary center of evolution within *Scytonotus*.

*Component. inornatus*, new species.

*Scytonotus inornatus*, new species

Figs. 17–18

*Type specimens*—Male holotype and one female paratype (FSCA) collected by J. Schuh, 25 October 1972, along a canal at Geary Ranch (exact location unknown), Klamath County, Oregon; four female paratypes (FSCA) taken by same collector at same locality on 28 October 1971.

*Diagnosis*—Tibiae of legs 13–20 in males with distal lobes; endomerite subequal in length to that of tibiotarsus; medial lamina expanding into large, broadly rounded flange for most of length, overhanging and extending well beyond inner margin of endomerite; distal lamina with inner margin smoothly linear, without denticulations or other modifications, outer margin narrowing abruptly to subacuminate termination with inner; lateral lamina long and narrow, expanding slightly proximad and distad but not overhanging inner margin of endomerite; paranota of segments 5–9 of females reduced.

*Description*—Head normal for genus, densely covered with short, fine, parallel-sided setae; epicranial suture distinct; genae extending well beyond adjacent cranial margins.

Collum much narrower than succeeding tergites, not covering epicranium, with about six transverse rows of setose tubercles, margins smooth. Remaining tergites with around four rows of setose tubercles, latter low and flattened, only slightly elevated above metatergal surface, poorly demarcated from each other; setae relatively long and slender, parallel-sided for most of length, tapering distad, many apically falcate, curving caudad. Paranota narrow but distinct, subparallel to substrate, margins lightly scalloped, notches sharpest on anteriormost tergites, vestigial on segments 5 and 9 and absent from segments 6–8 of females. Epiproct short, subtriangular, setae very long and conspicuous, tubercles barely detectable.

Sterna generally granular in appearance, without modifications, postgonopodal sterna with slight bicruciform impressions. Tibiae of 13th legs in males with short, glabrous spurs on outer margins; legs 12–15 with strong, rounded lobes in same locations; legs 16–18 with lobes diminishing progressively, absent on caudal legs.

Gonopodal aperture broad, obcordate, sides strongly elevated above metazonal surface. Gonopods in situ with telopodites leaning anteriad over coxae then curving broadly ventrocaudad over caudal margin of aperture, subparallel to each other. Gonopod structure as follows (Figs. 17–18). Coxa relatively small and narrow, with large lobe arising from medial surface extending over base of telopodite. Latter relatively small. Tibiotarsus of normal shape and appearance, curving broadly caudad. Endomerite subequal in length to that of tibiotarsus, closely appressed to latter for about half of length, diverging distad, with short, barbed, acicular projection arising basally on inner side of medial surface, terminating well short of outer margin of endomerite; inner surface with relatively long, sharply acuminate spur just distal to, and slightly shorter than, pulvillus, latter relatively long, narrowing slightly distad, apically blunt; medial lamina expanding rapidly into large, broadly rounded lobe, extending for most of length of structure, overhanging and extending well beyond inner margin of endomerite; distal lamina without modifications, inner and outer margins smoothly sublinear, latter angling rapidly to subacuminate termination with inner margin; lateral lamina relatively long, arising basally and extending for most of length of endomerite, expanding slightly proximad and distad.

*Ecology*—The available samples were taken from “mixed broadleaf duff.”

*Distribution*—Known only from Klamath County, Oregon (Fig. 20). The following sample was examined in addition to the types: Klamath Falls vic., F., March 1972, J. Schuh (FSCA).

*Remarks*—With no modifications on the distal lamina, only a broad flange on the medial one, and only two narrow expansions



on the lateral lamella, *S. inornatus* is the most pleisiomorphic known species. A hypothetical ancestral *Scytonotus* would resemble *S. inornatus* with a reduced medial lamina, and all other species of *Scytonotus* could have arisen from such an ancestral form. The species occurs east of the crest of the Cascade Mountains in the foothills on the boundary with the arid Basin and Range Physiographic Province. This area is much drier than those west of the crest where *S. simplex* and *bergrothi* occur. Presumably, the Geary Ranch is near Klamath Falls and is therefore in the Klamath River drainage, which flows westward and empties into the Pacific Ocean in southern Del Norte County, California.

*Scytonotus* sp.

To completely detail the generic distribution in the West, I record here the samples of *Scytonotus* that lack adult males and cannot be assigned to a species on a geographic basis. In Canada, coastal Washington, and Oregon, the records could refer to either *S. insulanus* or *bergrothi*, and the Stevens County, Washington, literature record (Causey 1954b) could be either *S. piger* or *S. columbianus*. These records are indicated by question marks in Figures 10 and 19-20.

CANADA: BRITISH COLUMBIA: VANCOUVER ISLAND: Courtenay, F, juv., June 1965, N. L. H. Kraus (NMNH). Robson Bight, Tsitika R., 2 juvs., 28 July 1986, D. H. & J. L. Kavanaugh (CAS). Little Qualicum Falls Prov. Pk., 2 juvs., 30 July 1989, R. M. Shelley (NCSM). 5 km NE Port Renfrew, 2F, 31 July 1989, R. M. Shelley (NCSM). Goldstream Prov. Pk., F, 2 August 1989, R. M. Shelley (NCSM).

MAINLAND SITES: Shannon Falls Prov. Pk., FF, juvs., 29 July 1989, R. M. Shelley, (NCSM). Along hwy. 99, 132 mi (21 km) N Squamish, FF, juvs., 29 July 1989, R. M. Shelley (NCSM). Capilano Cyn. Reg. Pk., 4F, 28 July 1989, R. M. Shelley (NCSM). 1.9 mi (3 km) SE Hope, along Silver Skagit Rd., F, 30 June 1988, S. & J. Peck (NCSM). Ten Mile, exact location unknown, juv., 20 June 1903, R. F. Currie (NMNH).

USA: WASHINGTON: Jefferson Co., Olympic Nat. Pk., Graves Cr. Cpgd., 2F, 25 August 1990, R. M. Shelley (NCSM). Grays Harbor Co., along Moclips R., 6.4 mi (10.2 km) W US hwy. 101, F, juv., 25 August 1990, R. M. Shelley (NCSM).

OREGON: Hood River Co., Perham Cr., 5F, 2 juvs., 4 August 1929, collector unknown (NMNH); and 4 mi (6.4 km) S Parkdale,

Dog R. Tr. #35, juv., 3 June 1991, R. M. Shelley (NCSM). *Douglas Co.*, Comstock, 4 juvs., 10 September 1935, R. V. Chamberlin (NMNH). *County Unknown*, Three Rocks, 2F, 31 May 1942, J. C. Chamberlin (NMNH).

Literature records to *Scytonotus* sp. by Causey (1954b) that cannot be assigned on a geographic basis are as follows:

USA: WASHINGTON: *San Juan Co.*, Doubleneck. *Snohomish Co.*, Edmonds. *Stevens Co.*, Evans.

## THE EASTERN SPECIES

### The *Granulatus* Group

#### *Scytonotus granulatus* (Say)

Figs. 21–22

*Polydesmus granulatus* Say, 1821:107. Gervais, 1847:104–105. Wood, 1865:214–215, fig. 41. Bollman, 1893:146. Kenyon, 1893*a*:161; 1893*b*:15.

*Scytonotus scabricollis* Koch, 1847:130; 1863:41–42, fig. 164. Bollman 1893:150–151. Attems, 1898:257; 1940:159.

*Scytonotus laevicollis* Koch, 1847:131; 1863:41, fig. 163. Bollman 1893:151. Cook and Cook, 1894:235. Attems, 1898:257; 1940:159.

*Scytonotus nodulosus* Koch, 1847:131; 1863:43, fig. 165. Bollman, 1893:122, 151. Cook and Cook, 1894:235–236. Attems, 1898:257; 1940:159. Bailey 1928:20. Chamberlin and Hoffman, 1958:76.

*Stenonia hispida* Sager, 1856:109.

*Polydesmus setiger* Wood, 1865:213–214. McNeill, 1888:5.

*Scytonotus cavernarum* Bollman, 1887:45; 1888*a*:407; 1893:122. Attems, 1898:257. Chamberlin and Hoffman, 1958:76.

*Scytonotus granulatus*: Bollman, 1887:47; 1888*a*:407; 1893:108, 122, 182, 184. Cook and Cook, 1894:238–246, pls. 6–9, figs. 1–41, 46–62, 64–71. Attems, 1898:256–257; 1940:156. Morse, 1902:187. Gunthorp, 1913:163. Bailey, 1928:20. Williams and Hefner, 1928:111, fig. 12B. Brimley, 1938:499. Dearolf, 1938:66. Chamberlin, 1928:155; 1940:56, 1942:16; 1947:24; 1952:558. Loomis, 1939:192. Rapp, 1946:666. Hoffman, 1950*a*:fig. 1; 1950*b*:30–31; 1962*b*:243–245, fig. 1. Causey, 1952:145; 1955:22. Johnson, 1954:248, figs. 23–24. Chamberlin and Hoffman, 1958:72–72. Wray, 1967:150. Shelley, 1978:61, figs. 48–49; 1988:1653, fig. 29. Filka and Shelley, 1980:25, fig. 41. Kevan, 1983:2969.

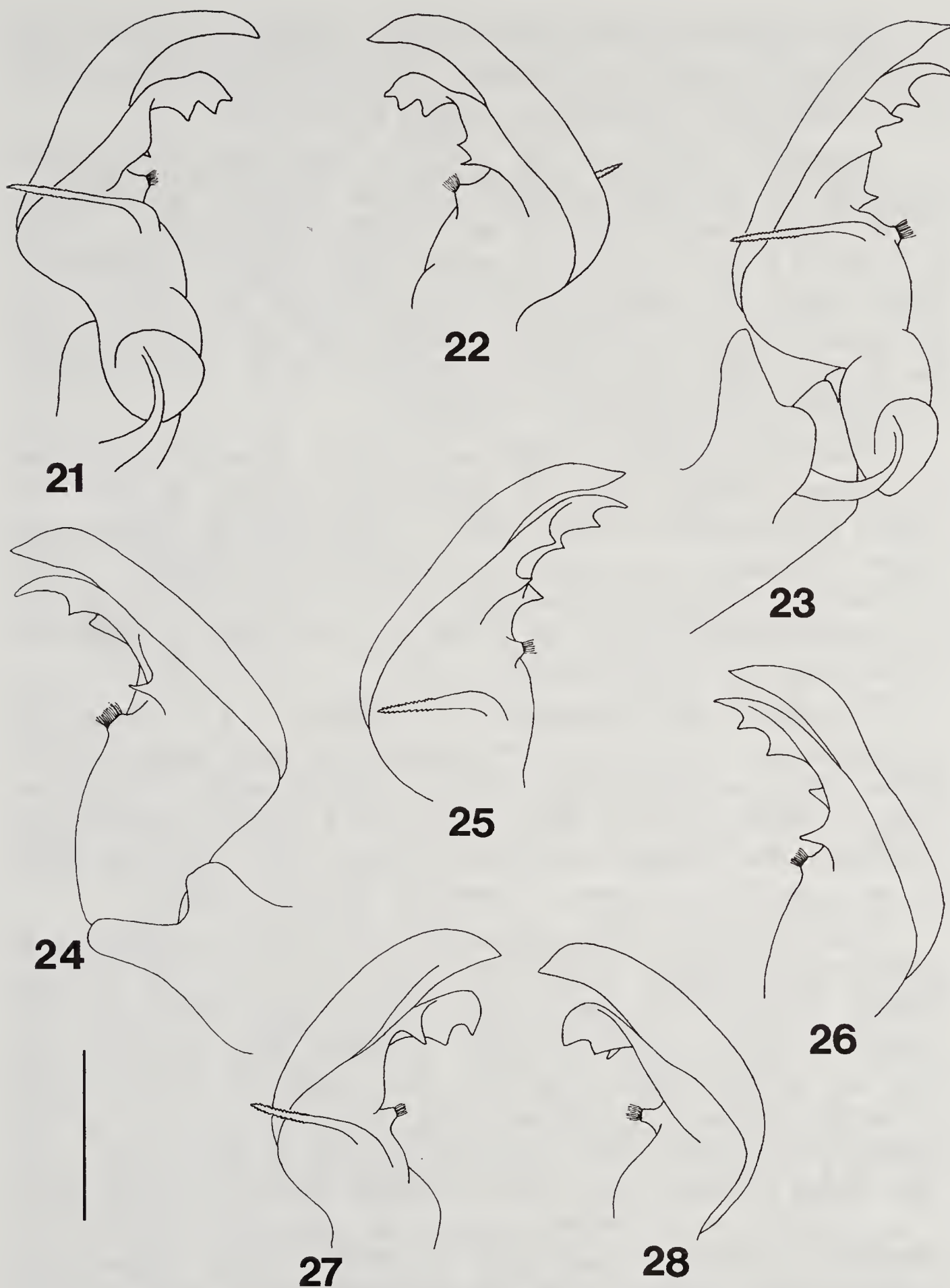
*Scytonotus setiger*: Bollman, 1888*b*:340. Cook and Cook, 1894:237.

*Scytonotus cavernarus*: Cook and Cook, 1894:237.

*Lasiolathus virginicus*: Loomis, 1944:175.

*Scytonotus* sp. Judd, 1967:192.





Figs. 21–28. 21–22, *S. granulatus*. 21, left gonopod of male from Dare County, North Carolina, medial view. 22, the same, lateral view. 23–24, *S. v. virginicus*. 23, left gonopod of male from Albemarle County, Virginia, medial view. 24, the same, lateral view. 25–26, *S. v. michauxi*. 25, telopodite of left gonopod of male from Yancey County, North Carolina. 26, the same, lateral view. 27–28, *S. austriallis*. 27, telopodite of left gonopod of male from Macon County, North Carolina, medial view. 28, the same, lateral view. Scale line = 0.5 mm for all figures.

*Type specimens*—Not known to exist, although part of the type series may be extant at the BMNH. The type locality is the vicinity of Philadelphia, Philadelphia County, Pennsylvania.

*Diagnosis*—Tibiae of legs 13–20 in males with distal lobes; tibiotarsus and endomerite essentially subequal in length, former slightly longer; medial lamina expanded into broadly rounded flange extending most of length of lamina, overhanging inner margin of endomerite; distal lamina with minute apical tooth preceded by two narrowly segregated teeth; lateral lamina expanding into narrow, flange, margin irregular, with one or two variable teeth (Figs. 21–22); females with paranota of segments 5–9 reduced.

*Variation*—Hoffman (1962*b*) noted that *S. granulatus* maintains its structural integrity over the entire range and that he could not discern geographically variable details. In spot-checking samples from across the range, I can corroborate Hoffman's observation: I found only minor differences in the sizes of the flanges on the medial and lateral laminae as well as in the size and degree of separation of the teeth on the distal lamina.

*Ecology*—I have encountered *S. granulatus* in a variety of microhabitats and believe it can be expected in most moist environments within its range; those with a preponderance of deciduous litter are more probable than those with a higher proportion of pine litter. The milliped will likely be found well within the litter, on the undersides of leaves or pieces of wood and bark.

*Distribution*—Covering almost the entire generic distribution in eastern North America, ranging from the vicinities of Trois Rivières, Quebec, and Sault St. Marie, Ontario, to central South Carolina, central Tennessee, and northeastern Arkansas, and east/west, from Vermont, coastal Virginia, and the Outer Banks of North Carolina to eastern Kansas and Nebraska (Fig. 29). The only part of the eastern generic range that is not inhabited by *S. granulatus* is the Blue Ridge Province from northern Virginia to north Georgia, where it is replaced by the endemic species, *S. virginicus* and *australis*. The distribution encompasses parts or all of a dozen physiographic provinces and 16 states, 6 of which—Pennsylvania, West Virginia, Kentucky, Ohio, Indiana, and Illinois—are wholly within its range. Specimens were examined as summarized below. Complete locality data are provided for states and Canadian provinces where *S. granulatus* is known from five or fewer counties; the latter are listed in alphabetical order when the milliped has been collected in more than five counties.

CANADA: QUEBEC: *Drummond Co.*, Drummondville, MM, FF,



4 April 1977, L. LeSage (NCSM). *Nicolet Co.*, Becancour, Bois de Fevillus, Erublet Tremble, MM, FF, 16 June 1979, L. LeSage (NCSM).

ONTARIO: *Algoma, Durham, Lanarck, Peterborough, Prescott and Russell*, and *York cos.* (CNC, GLFRS, NCSM, ROM).

USA: VERMONT: *Chittenden Co.*, Milton, M, 6 September 1975, J. Kantor (UVT). *Windsor Co.*, Hartland, M, 4 November 1961, D. P. Moorman (UVT).

NEW YORK: *Monroe Co.*, Ellison Park, M, F, 31 March 1963, collector unknown (NMNH). *Onandaga Co.*, Syracuse, M, F, 8 August 1960. L. C. Stegman (FSCA); and E. Onadaga, F, 15 September 1904, R. V. Chamberlin (MCZ). *Tompkins Co.*, Ithaca, along 6 Mile Cr., M, 8 May 1951, R. E. Crabill (VMNH). *Chemung Co.*, Elmira, M, 29 March 1948, R. E. Crabill (VMNH).

NEW JERSEY: *Essex Co.*, Caldwell, juvs., 12 April 1887, collector unknown (NMNH).

PENNSYLVANIA: *Armstrong, Berks, Bucks, Centre, Montgomery*, and *Washington cos.* (AMNH, ILNHS, MCZ, PSU).

MARYLAND: *Alleghany, Anne Arundel, Frederick, Garrett, Prince Georges*, and *Queen Annes cos.* (ILNHS, NCSM, NMNH, VMNH).

DISTRICT OF COLUMBIA: *Catholic Univ.*, 3M, 2F, April and October 1893, collector unknown (NMNH). *Glen Sligo*, F, April 1898, collector unknown (NMNH). *Rock Creek Park*, F, 8 November 1928, O. F. Cook (NMNH).

WEST VIRGINIA: *Gilmer Co.*, Cedar Creek St. Pk., M, 22 October 1969, collector unknown (NCSM). *Greenbrier Co.*, Greenbrier St. For., 2M, F, 28 April 1973, W. A. Shear (WAS). *Raleigh Co.*, Horse Cr., exact location unknown, juvs., 21 March 1966, J. Miller (WAS). *Monroe Co.*, nr. Greenville, along Laurel Cr., M, 16 April 1972, W. A. Shear (WAS). *Mercer Co.*, Speedway, along WV hwy. 20, M, F, 16 April 1966, J. Miller (WAS); and Athens, juvs., 16 May 1966, B. Carter (WAS), and M, 12 March 1967, W. A. Shear (WAS).

VIRGINIA: *Albemarle, Alleghany, Appomattox, Arlington, Augusta, Bath, Bland, Botetourt, Dickenson, Fairfax, Giles, Halifax, Mecklenburg, Prince Edward, Princess Anne, Pulaski*, and *York cos.* (AMNH, NCSM, NMNH, VMNH, WAS).

NORTH CAROLINA: *Beaufort, Cabarrus, Carteret, Chatham, Cumberland, Dare, Durham, Gaston, Guilford, Halifax, Harnett, Lincoln, Montgomery, Onslow, Orange, Person, Richmond, Rockingham, Stanly, Surry, Vance*, and *Wake cos.* (FSCA, NCSM, NMNH).

SOUTH CAROLINA: *Orangeburg Co.*, Orangeburg, F, 28

October 1929, O. F. Cook (NMNH).

MICHIGAN: *Presque Isle Co.*, Ocquecoco Falls, F, 11 July 1949, Etges (FSCA). *Livingston Co.*, E side George Res., M, 2F, 14 October 1949, K. Bohnsack (UMMZ) and 5 juvs., date unknown, E. Pruitt (MCZ). *Berrien Co.*, Stevensville Swamp, M, 4 May 1962, L. Lowry, H. Kamizge, W. Suter (FSCA); and Lakeside, Warren Woods, M, 3 October 1959, W. Suter (FSCA).

OHIO: *Wayne Co.*, Wooster and vic., MM, FF, juvs., 1959-1982, A. A. Weaver (NCSM). *Champaign Co.*, Pat Frances St. Mem., M, 1973, K. Menders (OHS). *Franklin Co.*, Snow Cave, M, 20 October 1979, M. Flynn (OHS). *Hocking Co.*, Cantwell Cliffs, M, 29 September 1963, F. A. Coyle (NCSM); and Rock House St. Pk., M, 21 April 1962, W. A. Shear (WAS). *Fairfield Co.*, Barnabey Ctr., 2M, 12 May 1984, collector unknown (SDMNH).

INDIANA: *Grant, Greene, Howard, Lawrence, Marion, Monroe, Newton, Porter, Putnam, Tippecanoe, and Wells cos.* (FSCA, ILNHS, MNHP, NMNH, UCD, UMMZ).

KENTUCKY: *Bell, Boyd, Carter, Edmonson, Estill, Fayette, Hart, Metcalf, and Wolfe cos.* (FSCA, ILNHS, NCSM, VMNH, WAS).

TENNESSEE: *Anderson, Bledsoe, Blount, Cumberland, Franklin, Knox, Roane, Sevier, and Washington cos.* (FSCA, MCZ, NMNH, VMNH).

WISCONSIN: *Adams, Crawford, Dane, Fon du Lac, Grant, Ozaukee, Rock, Richland, Sauk, Sheboygan, Trempealeau, Vernon, Walworth, and Washington cos.* (FSCA, ILNHS, MCZ, TMM, WAS).

ILLINOIS: *Alexander, Carroll, Champaign, Clark, Coles, Cook, Crawford, Jackson, Kendall, Lake, LaSalle, Logan, Madison, Mason, McLean, Peoria, Piatt, Pope, Putnam, Randolph, Richland, Union, Vermillion, and Winnebago cos.* (AMNH, EIL, ILNHS, ILSU, MCZ, NMNH, UCD, VMNH).

MINNESOTA: *Washington Co.*, along St. Croix R., 2M, 2F, 10 May 1941, M. Wing (UMN). *Hennepin Co.*, Minneapolis, FF, 1932, W. J. Gertsch (NMNH); and Ft. Snelling, M, F, date unknown, C. H. Bollman (NMNH) and M, 22 October 1931, A. C. Hodson (UMN). *Rice Co.*, Northfield, Carleton Arboretum, M, 11 October 1953, A. R. Brummett (FSCA). *County Unknown*. Tamarack Bog, M, F, 31 May 1931, A. C. Hodson (UMN).

IOWA: *Delaware Co.*, Backbone St. Pk., F, 28 August 1954, L. Hubricht (VMNH); and Colesburg, Ellis Park, F, 10 April 1983, collector unknown (MCZ). *Boone Co.*, Ledges St. Pk., M, 2 May 1961, D. P. Hansen (VMNH) and 2M, 3F, 10 April 1984, R. M. Shelley, R. L. Lewis (NCSM). *Storey Co.*, Ames, F, 27 April 1957, A. H. Barnum (DC).



MISSOURI: *Boone, Callaway, Chariton, Cole, Dent, and Phelps cos.* (AMNH, ANSP, FSCA, PSU).

ARKANSAS: *Craighead Co.*, Jonesboro, M, 26 November 1966, M. Hite (FSCA).

KANSAS: *Douglas Co.*, Lawrence, M, 18 December 1947, M. W. Sanderson (ILNHS).

The following additional literature records are deemed valid and are denoted by open symbols in Figure 29.

CANADA: ONTARIO: *Middlesex Co.*, London and vic. (Judd 1967).

USA: VIRGINIA: *Montgomery Co.*, Elliston (Hoffman 1947).

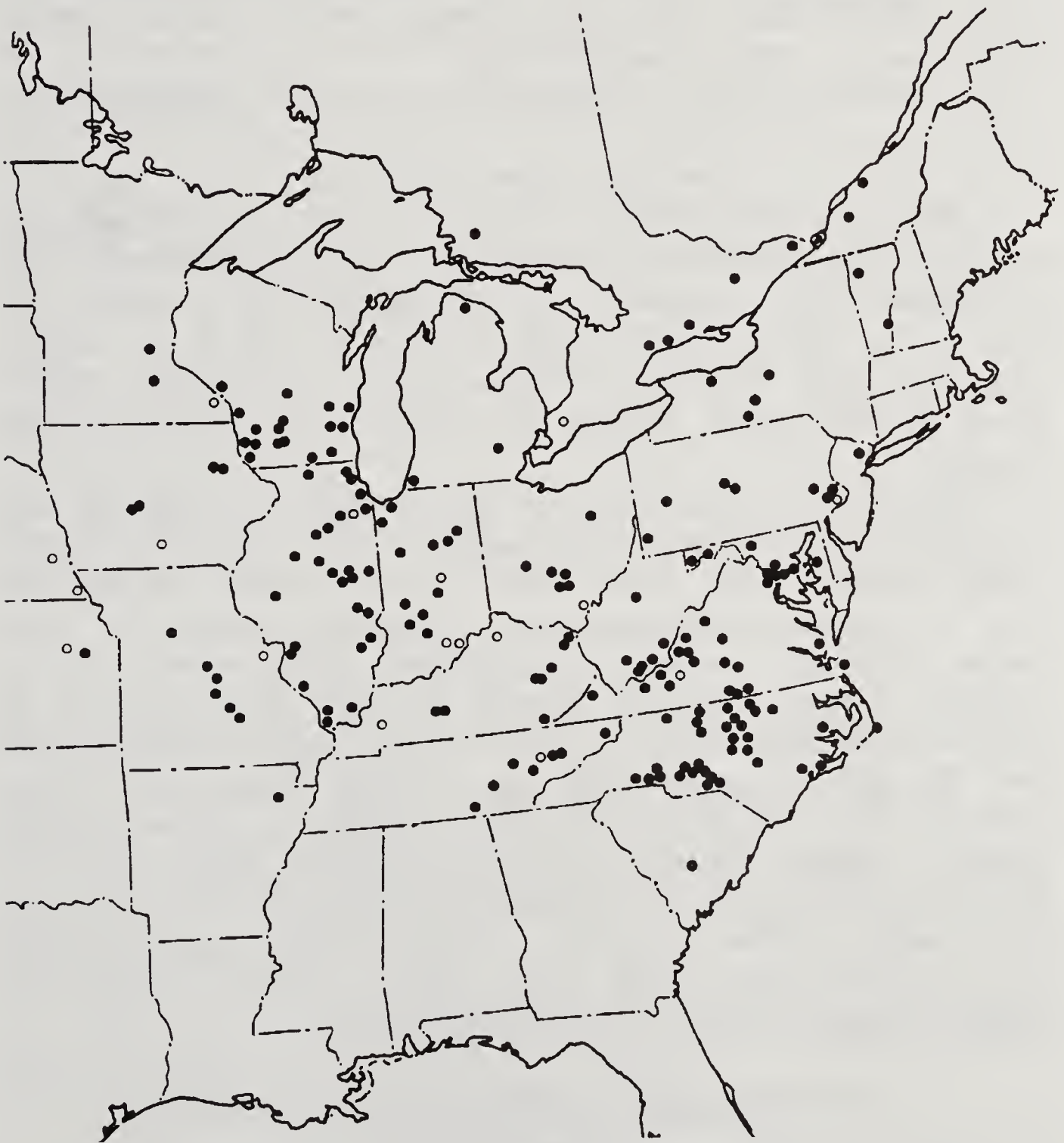


Fig. 29. Distribution of *S. granulatus*.

INDIANA: *Clark Co.*, New Providence (Bollman 1888a). *Hamilton Co.*, Westfield (Bollman 1888a). *Washington Co.*, Salem (Bollman 1888a).

OHIO: *Gallia Co.*, Vinton (Morse 1902).

KENTUCKY: *Grant Co.*, Crittenden (Loomis 1944, Hoffman 1947). *Hopkins Co.*, Nortonville (Causey 1955). *County unknown*, Indian Cave (Dearolf 1938).

TENNESSEE: *Jefferson Co.*, Mossy Cr. (Bollman 1888b).

ILLINOIS: *Will Co.*, Monee (Chamberlin 1952).

MINNESOTA: *Winona Co.*, Winona (Bollman 1893).

IOWA: *Warren Co.*, Indianola (Chamberlin 1942).

MISSOURI: *St. Charles Co.*, St. Charles (Chamberlin 1928).

NEBRASKA: *Cass Co.*, Weeping Water (Kenyon 1893b). *Richardson Co.*, Rulo (Kenyon 1893b).

KANSAS: *Shawnee Co.*, locality not specified (Gunthorp 1913).

### *Scytonotus virginicus* (Loomis)

*Diagnosis*—Tibiae of legs 13–20/22 of males without distal lobes; tibiotarsus and endomerite subequal in length; medial lamina with two distinct teeth, segregated to varying distances; distal lamina with two or three teeth, an apical tooth followed by one or two moderately segregated teeth; lateral lamina varying in length but with a strong proximal spine; females with paranota of segments 5–9 not reduced.

*Remarks*—Hoffman (1962b) distinguished *S. virginicus* and *michauxi* by the degree of segregation of the teeth on the medial lamina (narrow in the former, wide in the latter) and by the presence of two (*virginicus*) or three (*michauxi*) teeth on the distal lamina. Although Chamberlin and Hoffman (1958) reported that *S. virginicus* ranged southward through the Blue Ridge Province to Linville Falls, Burke County, North Carolina, Hoffman (1962b) stated that the species was unknown on the Blue Ridge south of the Roanoke River and assigned the name *michauxi* to forms in North Carolina. Material secured in the past 30 years shows that these two forms intergrade in southwestern Virginia from Mt. Rogers, Grayson County, to Pinnacles of Dan, Patrick County, and hence that they are only subspecifically related. As *S. virginicus* is the older name, *michauxi* is reduced to subspecific status.

*Scytonotus virginicus virginicus* (Loomis), new status

Figs. 23–24

*Lasiolathus virginicus* Loomis, 1943:319–320, fig. 1.

*Scytonotus granulatus* (nec Say): Hoffman, 1947:140.



*Scytonotus virginicus*: Hoffman, 1950a:220; 1962b:247, fig. 5. West, 1953:123–176, figs. 1–41. Chamberlin and Hoffman, 1958:73.

*Type specimens*—Juvenile male holotype (MCZ) and one juvenile male paratype (NMNH) collected by H. F. and E. M. Loomis, 13 July 1937, at Thornton Gap, Page/Rapahannock counties, Virginia.

*Diagnosis*—Teeth on medial lamina narrowly segregated; distal lamina with two teeth; lateral lamina relatively short, terminating well short of midlength of endomerite (Figs. 23–24.).

*Ecology*—Expected in moist litter anywhere within the known range, hardwood detritus being more likely than pine.

*Distribution*—The Blue Ridge Province of Virginia from Warren to Bedford counties including Shenandoah National Park (Fig. 30). Specimens were examined as follows:

VIRGINIA: *Warren Co.*, Shenandoah Natl. Pk., N end of Skyline Dr., MM, FF, 24 September 1945, collector unknown (NMNH). *Page/Rapahannock cos.*, Thornton Gap, off US hwy. 211, Shenandoah Nat. Pk., M, 29 March 1949, R. L. Hoffman (VMNH) TYPE LOCALITY. *Albemarle Co.*, Sugar Hollow, 6 mi. (9.6 km) W Whitehall, 6M, 10F, juv., 21 March and 9 April 1949, R. L. Hoffman (VMNH). *Nelson Co.*, 4 mi (6.4 km) S Afton, Humpback Mtn. M, F, 14 October 1948, R. L. Hoffman (VMNH). *Botetourt Co.*, 2 mi (3.2 km) E Arcadia, jct. VA hwys. 59 and 782, F, 6 March 1976, R. L. Hoffman (VMNH); and 1.3 mi (2.1 km) E Arcadia, along North Cr., 2M, 2F, 13 October 1973, R. L. Hoffman (VMNH). *Bedford Co.*, Flat Top Mtn., 4M, 5F, 15 April 1951, L. Hubricht (VMNH); and Peaks of Otter, M, 15 October 1955, R. L. Hoffman (NMNH).

*Scytonotus virginicus michauxi* Hoffman, new status

Figs. 25–26

*Scytonotus granulatus* (nec Say): Chamberlin, 1940:56. Wray, 1950:150; 1967:150.

*Scytonotus virginicus* (nec Loomis): Wray, 1950:150; 1967:150.

*Scytonotus michauxi* Hoffman, 1962b:247–249, fig. 6.

*Type specimens*—Male holotype and one male paratype (NMNH) collected by L. Hubricht, 26 June 1950, on Roan Mountain, Carter County, Tennessee.

*Diagnosis*—Teeth on medial lamina widely separated; distal lamina with three teeth; lateral lamina relatively long, extending well beyond midlength of endomerite (Figs. 25–26).

*Ecology*—Same as for the nominate subspecies.

*Distribution*—The Blue Ridge Province of North Carolina and Tennessee from the Virginia state line to the Great Smoky Mountains (Fig. 30). Specimens were examined as follows:

NORTH CAROLINA: *Ashe Co.*, 2.8 mi (4.5 km) W Warrentonville, M, 5F, 18 October 1953, L. Hubricht (VMNH). *Watauga Co.*, Blowing Rock, Residence on Goforth Rd., 0.5 mi (0.8 km) N US hwy. 321, juvs., 16 October 1971, R. M. Shelley (NCSM). *Avery Co.*, Linville, Grandfather Mtn., M, 2F, 1939, collector unknown (NMNH). *Burke Co.*, Linville Falls, M, 7 April 1949, D. L. Wray (VMNH). *Mitchell Co.*, Summit of Roan Mtn., M, 11 October 1975, J. C. Clamp (NCSM); and Roan Mtn., below Carver's Gap, along NC hwy. 261, M, F, juvs., 23 September 1950, L. Hubricht (VMNH). *McDowell Co.*, nr. entrance to Black Mtn. cpgd. off NC hwy. 80, M, F, 11 October 1975, J. C. Clamp (NCSM). *Yancey Co.*, Stepps Gap, Black Mtns. 2M, F, 26 May 1962, L. Hubricht (VMNH); Crabtree Meadows Rec. Area along Blue Ridge Pkwy., 4M, 6F, 30 October 1971, R. L. Hoffman, L. S. Knight (VMNH); and Mt. Mitchell, M, F, 17 August 1955, A. Van Pelt (VMNH), MM, F, 16 October 1965, J. & W. Ivie (AMNH), MM, FF, 1 November 1969, W. A. Shear (WAS), and 3M, 13 May 1970, F. A. Coyle (NCSM). *Madison Co.*, 0.5 mi (0.8 km) W Windy Gap, E of Faust, F, 13 September 1952, L. Hubricht (VMNH). *Swain Co.*, Great Smoky Mtns. Nat. Pk. precise locality unknown, M, 20 May 1961, R. E. Woodruff (FSCA).

TENNESSEE: *Carter Co.*, Roan Mtn., 8M, 5F, 26 June 1950, L. Hubricht (NMNH, VMNH) TYPE LOCALITY; and 1 mi N. Hampton, Doe R. Bluffs, M, 3 May 1951, L. Hubricht (VMNH). *Sevier Co.*, Great Smoky Mtns. Nat. Pk., Rainbow Falls Tr., 27 September 1978, G. Summer (NCSM); and 2 mi (3.2 km) NNW Newfound Gap, 6M, F, 13 October 1970, W. A. Shear (WAS).

#### *Scytonotus virginicus* intergrades

The intergrade specimens are quite variable. Some have only an intermediate degree of segregation of the teeth on the medial lamina, whereas others have the characters of one race on the medial lamina and those of the other on the distal lamina.

*Distribution*—The southern extremity of the Blue Ridge Province in Virginia (Fig. 30). Specimens were examined as follows:

VIRGINIA: *Smythe Co.*, north side of Whitetop Mtn., along VA hwy. 600, 2M, 2F, 4 May 1964, R. L. Hoffman (VMNH). *Grayson Co.*, S slope of Mt. Rogers, 3M, 2F, juv., 20 October 1963, R. L. Hoffman (VMNH). *Wythe/Grayson cos.*, vic. of Comer's Rock, Iron Mtn. M, 12 December 1965, R. L. and L. Hoffman (VMNH). *Patrick Co.*, 4 mi (6.4 km) SW Vesta, Pinnacles of Dan, M, 9 April 1978, R. L. Hoffman (VMNH).



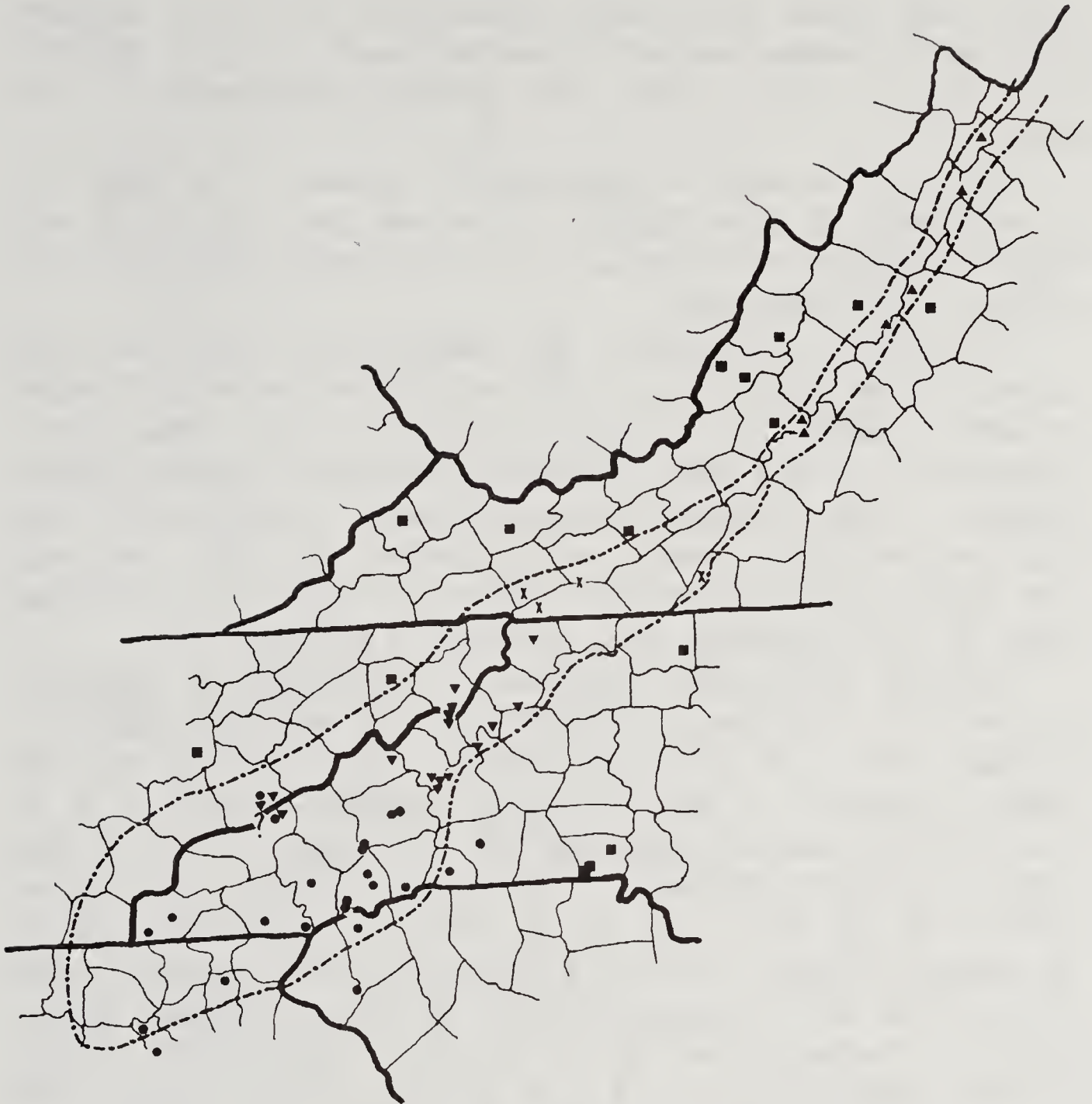


Fig. 30. Distributions of *Scytonotus* spp. in and near the Blue Ridge Physiographic Province; some symbols denote more than one locality. Squares, *S. granulatus*; upright triangles, *S. v. virginicus*; inverted triangles, *S. v. michauxi*; X's, *S. virginicus* intergrades; dots, *S. australis*; question mark, *S. australis* x *v. michauxi* hybrid.

*Scytonotus australis* Hoffman

Figs. 27–28

*Scytonotus granulatus* (nec Say): Hoffman, 1950b:30-31.

*Scytonotus australis* Hoffman, 1962b:245–247, fig. 4.

*Type specimens*—Male holotype and one female paratype (NMNH) collected by L. Hubricht, 6 November 1960, from a ravine 6 mi (9.6 km) W Amicalola Falls, Dawson County, Georgia.

*Diagnosis*—Tibiae of legs 13–20/22 of males without distal lobes; tibiotarsus slightly longer than endomerite; medial lamina moderately expanded basally, with or without strong indentation at midlength,

with strong apical tooth; distal lamina with two broad, subequal teeth; lateral lamina narrowly expanded basally, without modifications (Figs. 27–28); females with paranota of segments 5–9 not reduced.

*Ecology*—As with the other eastern species, *S. australis* may be anticipated in moist habitats throughout its range, those with higher proportions of deciduous trees being more likely than those that are predominantly pine.

*Distribution*—The southern Blue Ridge Province from Buncombe County, North Carolina, to White and Dawson counties, Georgia, extending westward to the western periphery of the Great Smoky Mountains in Sevier County, Tennessee, and eastward onto the western periphery of the Piedmont Plateau in Oconee County, South Carolina, and Rutherford County, North Carolina (Fig. 30). The range very slightly overlaps the southern extremity of that of *S. v. michauxi* (Figs. 30, 32). Specimens were examined as follows:

NORTH CAROLINA: *Buncombe Co.*, Asheville, F, 5 September 1961, R. L. Hoffman (VMNH); 4 mi (6.4 km) N Oteen, M, 16 October 1975, J. & W. Ivie (AMNH); and 20 mi (32 km) SW Asheville, foothills nr. Mt. Pisgah, M, 15 October 1965, J. & W. Ivie (AMNH). *Buncombe/Haywood cos.*, Mt. Pisgah, M, 4F, 7 April 1949, D. L. Wray (VMNH). *Henderson Co.*, Tuxedo, along co. rd. 1852, 6 mi (9.6 km) N jct. co. rd. 1850, M, 30 October 1975, R. M. Shelley (NCSM). *Polk Co.*, 2 mi (3.2 km) NW Columbus, along co. rd. 1136, M, 15 October 1973, R. M. Shelley (NCSM). *Rutherford Co.*, Rutherfordton, F, 15 October 1973, R. M. Shelley (NCSM). *Transylvania Co.*, 4.9 and 5.7 mi (7.8 and 9.1 km) NW Brevard, 2M, 2F, 29 August 1973, R. M. Shelley (NCSM); nr. L. Toxaway, head of Thompson R. Gorge, 30 juvs., 5 September 1961, R. L. Hoffman (VMNH); and 12 mi (19.2 km) SW Rosman, along co. rd. 1152, 0.8 mi (1.3 km) N jct. co. rd. 1151, F, 28 August 1973, R. M. Shelley (NCSM). *Jackson Co.*, Wolf Cr. Biol. Pres., Cullowhee Mtn. Rd., M, 10 June 1970, F. A. Coyle (NCSM). *Macon Co.*, Highlands, 6M, 10F, 19 October and 16 November 1961, R. L. Hoffman (VMNH); and Coweeta Hydrologic Sta., 4M, 3F, 27 September 1964, H. R. Steeves (FSCA) and M, F, 31 March–28 April 1978, L. Reynolds (NCSM). *Swain Co.*, 0.5 mi (0.8 km) N Oconoluftee Ranger Sta., Mingus Mill Cr., Great Smoky Mtns. Nat. Pk., 2M, 3F, 23 November 1973, F. A. Coyle (NCSM). *Cherokee Co.*, 7.2 mi (11.5 km) NW Murphy, along co. rd. 1326, 0.3 mi. W jct. co. rd. 1406, juv., 27 July 1974, R. M. Shelley (NCSM); and 7.7 mi (12.3 km) WNW Culberson, along co. rd. 1137, 0.6 mi W jct. US hwy. 64, F, 27 July 1974, R. M. Shelley (NCSM).



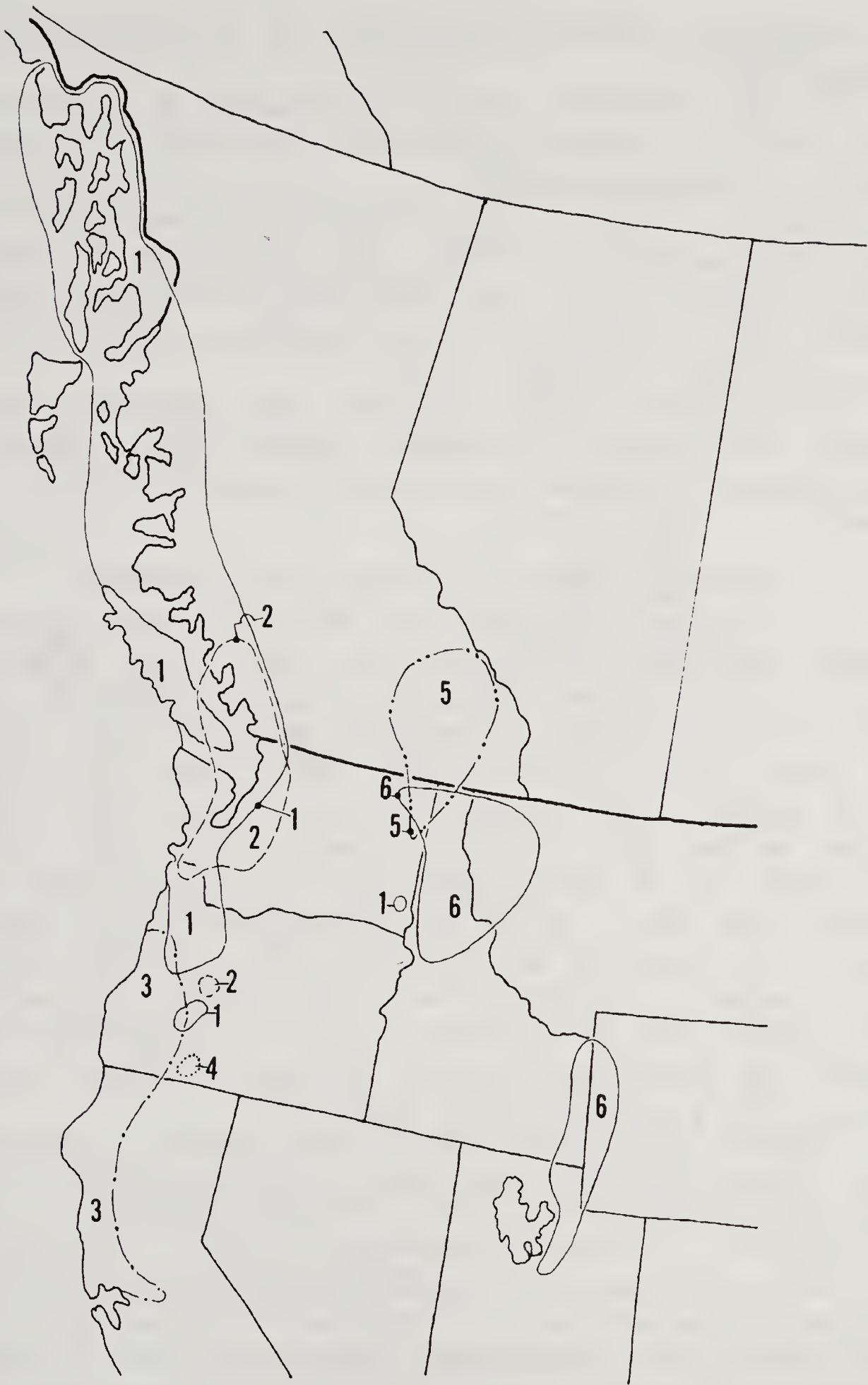


Fig. 31. Comparative distributions of species of *Scytonotus* in western North America. 1, *insulanus*; 2, *bergrothi*; 3, *simplex*; 4, *inornatus*; 5, *columbianus*; 6, *piger*. The boundary line of *S. insulanus* is continued through the ocean off British Columbia and Alaska to show that the distribution excludes the Queen Charlotte Islands.

TENNESSEE: *Sevier Co.*, Gatlinburg, M, F, date and collector unknown (NMNH).

SOUTH CAROLINA: *Oconee Co.*, Clemson, F, 22 December 1966, J. A. Payne (VMNH). *Pickens Co.*, Burnt Mtn., F, 6 November 1960, L. Hubricht (VMNH).

GEORGIA: *White Co.*, 2.7 mi (4.3 km) N Robertsville, F, 12 March 1961, L. Hubricht (VMNH). *Dawson Co.*, 6 mi (9.6 km) W Amicalola Falls, 3M, 8F, 6 November 1960, L. Hubricht (NMNH, VMNH) TYPE LOCALITY; and 6 mi (9.6 km) SW Dawsonville, F, 8 April 1961, L. Hubricht (VMNH).

*Remarks*—The record of juveniles from Highlands, Macon County, North Carolina, that Hoffman (1950*a*, 1962*b*) assigned to *S. granulatus* and *michauxi*, respectively, is properly referable to *S. australis*.

*Scytonotus australis* X *S. virginicus michauxi* hybrid

The gonopods of a male from the Great Smoky Mountains National Park, North Carolina/Tennessee, show features of both *S. australis* and *v. michauxi*. The distal lamina is clearly that of the former; the lateral lamina is clearly that of the latter; and the medial lamina combines aspects of both, with a distal tooth like that of the population of *S. australis* in the "Smokies," and with a smaller, proximal tooth so that the lamella has two teeth as in *S. v. michauxi*. As all other samples from this area are clearly one species or the other, I do not think this one individual suffices to overturn my conclusion that these forms are specifically distinct; hence, I record it as a hybrid. The sample emphasizes the need for more material from the borderline counties in southwestern North Carolina and southeastern Tennessee. Data are as follows: the site is denoted by a question mark in Figure 30.

NORTH CAROLINA/TENNESSEE: *Swain/Sevier cos.*, Clingman's Dome summit, M, F, 24 October 1969, W. A. Shear (WAS).

Distribution

The generic range is characterized earlier in this work and need not be repeated, but it is informative to examine the distributions of the species and lineages (Figs. 31–33), and their spatial relationships. As shown in Figures 31–32, the species-group taxa demonstrate allopatric and parapatric spatial relationships with minimal range overlaps, except for the high level of sympatry between *S. insulanus* and *bergrothi* (Fig. 31, nos. 1 and 2, respectively) on Vancouver Island, the southwestern mainland of British Columbia, and western Washington. Large gaps exist between *S. granulatus* in the east and *S. piger* in the west (about 984 mi [1590 km]),



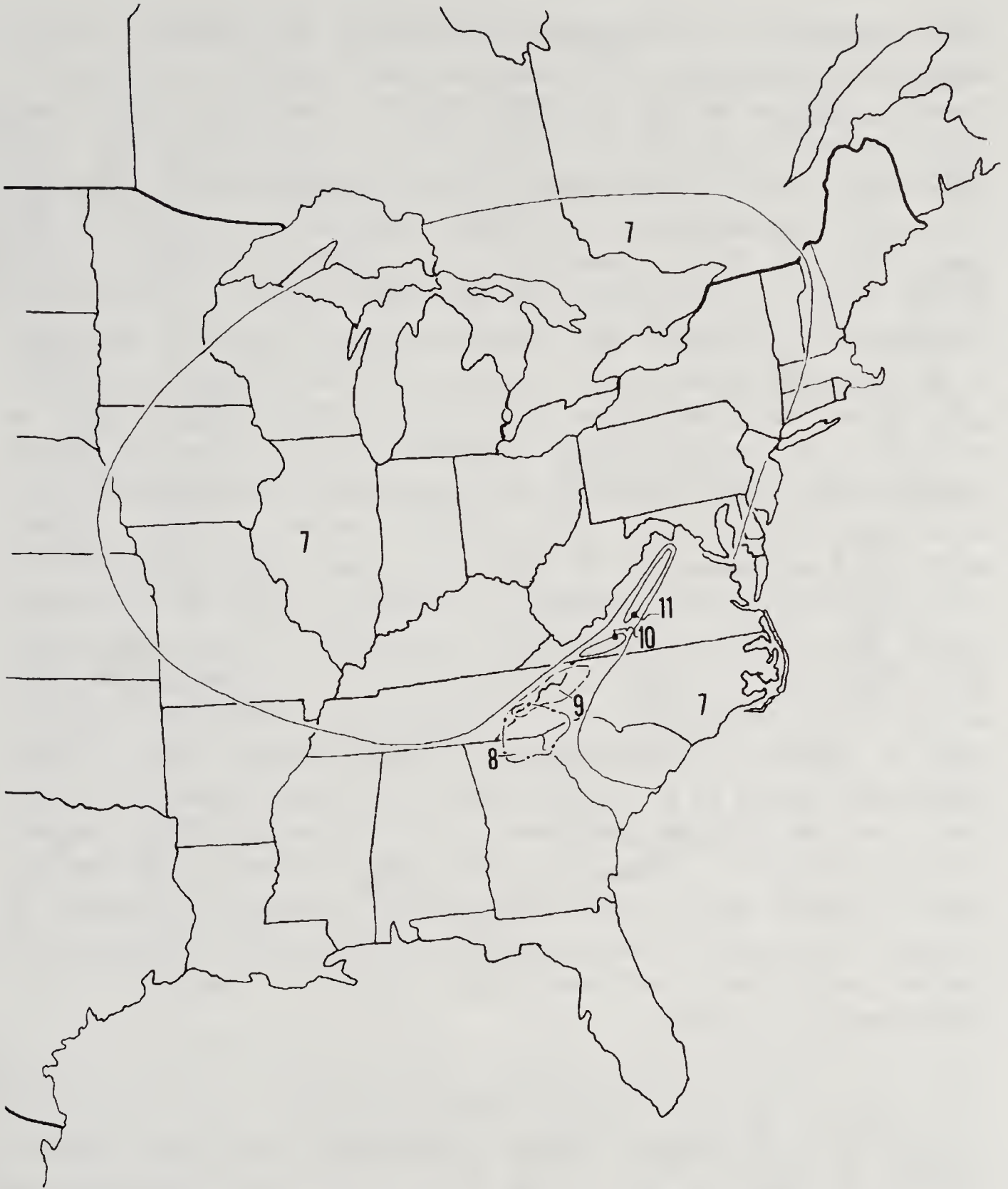


Fig. 32. Comparative distributions of species and subspecies of *Scytonotus* in eastern North America. 7, *granulatus*; 8, *australis*; 9, *v. michauxi*; 10, *v. virginicus*; 11, *virginicus* intergrades.

between the two areas occupied by *S. piger* (approximately 274 mi [438 km]), and between the main range and the allopatric population of *S. insulanus* in southeastern Washington (around 208 mi [333 km]). Smaller distances separate apparently allopatric populations of *S. insulanus* and *bergrothi* in Oregon's Lane and Douglas counties, respectively, from the main areas of their ranges. *Scytonotus* is therefore cohesive along the Pacific Coast and demonstrates attributes of a small mosaic (see Shelley and Whitehead 1986, Shelley

1989), although it is beginning to fragment as evidenced by the segregated populations of *S. insulanus* and *bergrothi*. *Scytonotus* is likewise cohesive in the east, particularly in the Blue Ridge Province, but the overall generic picture is so dominated by the three large lacunae and the three areas of the *granulatus* group (Fig. 33), as to create the impression of a highly dissected taxon. The *bergrothi* group, the only lineage west of the Cascades, is restricted to the Pacific Coastal region aside from the small area of *S. insulanus* in southeastern Washington; the *inornatus* group, essentially parapatric to the *bergrothi* group and *S. simplex*, and the allopatric *granulatus* group cover the other areas east of the Cascades. The absence of lacunae in the *bergrothi* group, in contrast to the *granulatus* group, suggests more recent evolution. The essentially parapatric occurrence of *S. inornatus*, the most plesiomorphic species, coupled with the nearly total dominance of the *granulatus* group to the east, point to the general area of the Cascades in southern Oregon as the primary source area or center of evolution. A secondary center exists in the Blue Ridge Province, and the distribution of *S. granulatus* appears to have been “unzipped” in a northeastwardly direction along the spine of the Blue Ridge beginning in north Georgia (Fig. 32). The greater distribution of *S. australis* and its spreading beyond the mountains onto the western periphery of the Piedmont Plateau suggest that it evolved first among the Blue Ridge endemics and has had time to expand and to attain reproductive isolation. In contrast, its younger counterparts to the north are still linked by intergrades and display progressively narrower ranges within the confines of this physiographic province.

### Relationships

*Generic*—A cladistic analysis of genera in the Polydesmidae is beyond the scope of this work and is also impossible today, as many genus-group taxa are poorly known and consist of only one or two species. Many decades will doubtlessly pass before the alpha taxonomy of the family is sufficiently stable to allow such an effort. Hoffman (1979) did not even attempt to divide the family into subfamilies, merely listing the component genera in alphabetical order and inadvertently omitting two monobasic ones: *Mastodesmus* Carl, 1911, from Java, as noted by Golovatch (1991), and *Alpertia* Loomis, 1972, from Washington state, United States. Consequently, only the most tenuous surmisals are possible about the affinities of *Scytonotus*. With two branches to the telopodite, it differs from the other native Nearctic polydesmid genera, so its relationships must lie with taxa on other continents, and Cook (1911) suggested, but





Fig. 33. Comparative distributions of species groups of *Scytonotus*. 1, the *inornatus* group; 2, the *bergrothi* group; 3, the *granulatus* group. The boundary line of the *bergrothi* group is continued through the ocean off British Columbia and Alaska to show that the range excludes the Queen Charlotte Islands.

did not formally propose, separate family status. Hoffman (1962b) mentioned that this two-branched development might be homologous to that in some European species of *Polydesmus*, for example *P. inconstans* Latzel, which has been introduced into North America and occurs in many American and Canadian cities. Golovatch (1991) suggested that the Asian genera *Schizoturanus* Verhoeff and *Turanodesmus* Lohmander, from Kirgizstan and Turkestan, respectively, might be allied to *Scytonotus* because they also possess the two-branched structure. As illustrated by Attems (1940), the gonopods of *T. stummeri* (Attems) and *T. inermis* Lohmander resemble the basic structure of *Scytonotus*, so Golovatch's idea seems plausible

and should be evaluated when an analysis of the Polydesmidae becomes possible.

*Specific*—The species groups, or major components, are natural entities that could be regarded as subgenera, and all three could conceivably have arisen from an ancestral form similar to *S. inornatus*, considered the most plesiomorphic species because of the unmodified distal and lateral laminae. Evolution of the toothed and prolonged conditions of the distal lamella from such a nondescript structure is easily envisioned, whereas it is difficult to imagine the reverse, with either of the former configurations giving rise to the other. I therefore consider the *inornatus* group as sister to the *bergrothi* + *granulatus* lineage. Within the *bergrothi* group, I am unable to resolve relationships between *S. insulanus*, *bergrothi*, and *simplex*, which are shown as a trichotomy in Figure 34. Within the *granulatus* group, I consider the “normal” male tibiae and female paranota, and the toothed medial laminae to be synapomorphies uniting *S. australis* + *virginicus* as a sister clade to *S. granulatus*. The “normal” male tibiae and female paranota of *S. columbianus*, convergent with these features in the Blue Ridge endemics, are also apomorphic for this species. No apomorphies are known for *S. piger* and *granulatus*, but they are supported by geographic cohesiveness as discussed by Shelley and Whitehead (1986) for the xystodesmid genus *Sigmoria*. I therefore believe that relationships within this line are *columbianus* + (*piger* + (*granulatus* + (*virginicus* + *australis*))) (Fig. 34).

## CONCLUSION

As stated previously, the geographical locations of the lineages coupled with the ancestral phylogenetic position of *S. inornatus* point to the general area of the Cascade Mountain Range in southern Oregon as the primary center of evolution within the genus. A secondary center exists in the Blue Ridge Province, as the younger and possibly more successful endemic species appear to have displaced *S. granulatus* from these mountains and to be expanding into adjacent physiographic provinces. Thus, although the evidence in *Scytonotus* supports Hoffman's contention (1969) that Appalachia, or in this case the Blue Ridge Province specifically, is an important evolutionary and dispersal center, analysis of the entire genus leads to the opposite conclusion regarding the relative ages of the eastern species. The broad occurrence of *S. granulatus* east of the Plains, including areas west of the Mississippi River, represents fragmentation of an ancient range that extended west of the Continental Divide, and *S. granulatus* and *piger* were doubtlessly connected in the past. *Scytonotus granulatus* is thus much older than the Blue



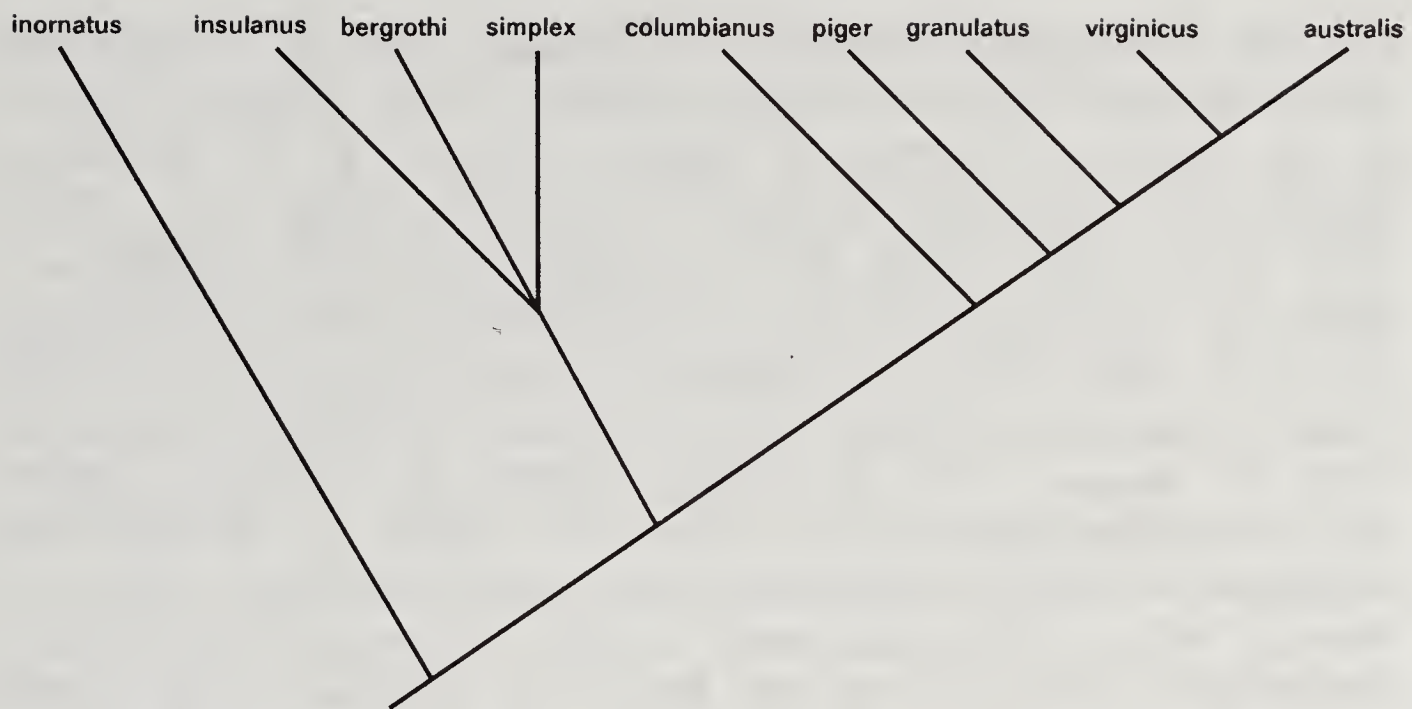


Fig. 34. Hypothesized relationships in *Scytonotus*.

Ridge endemics, which rather than being old forms relegated to relict statuses and restricted distributions in the Appalachians as suggested by Hoffman (1969), are really young, derivative entities. The absence of *S. granulatus* from the Blue Ridge suggests displacement by the endemics, and future displacement could occur in surrounding areas, as they expand their ranges. This process has already begun in the south, as *S. australis*, probably the oldest endemic, has spread beyond the Blue Ridge escarpment and apparently eradicated *S. granulatus* from the western periphery of the Piedmont Plateau in the Carolinas and north Georgia.

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# New Molluscan (*Gastropoda* and *Bivalvia*) Records for the Neuse River Basin, North Carolina

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**ABSTRACT**—Twenty-three species of molluscs were collected from the Piedmont area of the Neuse River basin in North Carolina. Thirteen species of gastropods and ten bivalves (six sphaeriids and four unionids) were collected. New distribution records for six species are reported: *Ferrissia fragilis*, *Laevapex fuscus*, *Gyraulus deflectus*, *Planorbella trivolvus*, *Musculium securis*, and *Pisidium variable*.

Walter (1956) conducted the first intensive molluscan survey in North Carolina. This was the only survey conducted in the Neuse River basin. In the past 37 years only incidental sampling has taken place while the Neuse area has undergone rapid urbanization and industrialization which have affected aquatic habitats and have undoubtedly altered molluscan communities. Mounting concern among malacologists about the impact of anthropogenic changes on molluscan populations led the Scientific Council of Freshwater and Terrestrial Mollusks to recommend that surveys be performed to determine species distributions (Adams et al. 1990). From October 1989 to October 1990, we resurveyed some of the upper or Piedmont portion of the Neuse drainage.

## METHODS

Molluscs were collected from 50 stations in the Piedmont area of the Neuse River basin of North Carolina. North Carolina Department of Transportation County Road Maps (revised 1988) were used to select 10 stations from each of five counties (Durham, Franklin, Johnston, Wake, and Wilson). Stations were explored from October 1989 to October 1990. Most collections occurred during summer and early fall 1990 when molluscs were most abundant.

Molluscs were collected by hand from the littoral zones of streams and ponds, from rocks in erosional zones of streams, and from the banks and bottoms of shallow streams. A dip net was used to sift the bottom substrate of deeper waters.

Snails and mussels were initially identified with the use of Environmental Protection Agency keys to "Freshwater Unionacean Clams (Mollusca: Pelacypoda) of North America" and "Freshwater

Snails (Mollusca: Gastropoda) of North America" (Burch 1973, 1982), respectively. William F. Adams (Army Corps of Engineers, Wilmington, North Carolina) verified these identifications. The sphaeriacean clams were identified by Gerald L. Mackie (University of Guelph, Ontario, Canada).

Specimens were retained in the author's collection for further study.

## RESULTS AND DISCUSSION

Twenty-three species of molluscs (13 gastropods and 10 bivalves) were collected from the upper Neuse River and its tributaries. This note reports only the six species that have not been previously recorded from the Neuse River system.

*Ferrissia fragilis* (Tryon, 1863) (Gastropoda: Pulmonata: Ancyliidae) was encountered at 12 stations in five counties—Wilson, Franklin, Johnston, Wake, and Durham—primarily on debris (wood and leaves) and macrophytes of the littoral zone in lentic and lotic habitats. *Ferrissia hendersoni* (Walker, 1908), previously reported from the Neuse basin by Walter (1956) and Dawley (1965) and listed as a species of special concern (Adams et al. 1990), was not found. Basch (1963) considered *F. hendersoni* to be a variant of the "super species" *F. fragilis*; thus, further research and taxonomic clarifications are needed to determine the actual status of these two limpet snails.

Another limpet, *Laevapex fuscus* (Adams, 1841) (Gastropoda: Pulmonata: Ancyliidae), was taken from rocks and debris in Wilson, Franklin, and Durham counties. Previously, *Laevapex diaphanus* (Haldeman, 1841) (Gastropoda: Pulmonata: Ancyliidae) was reported from 22 stations in the Neuse River basin (Walter 1956); we did not find it during our survey. Although Basch (1963) reported the distribution of *F. fragilis* to be widespread throughout North America and *L. fuscus* to occur within the southeastern states, this is the first report of these two limpet snails from the Neuse drainage, specifically.

We collected the large planorbid, *Planorbella trivolvis* (Say, 1817) (Gastropoda: Pulmonata: Planorbidae), from wood and leaf substrates at two lotic stations in Franklin and Johnston counties, located on the Little River at US 401 and Cattail Creek at SR 1738, respectively. Other published reports of *P. trivolvis* from North Carolina include Lake Waccamaw (Pilsbry 1934) and Greenfield Lake (Adams 1990).

Powell's Pond at SR 2227 in eastern Wake County was the only station from which *Gyraulus deflectus* (Say, 1824) (Gastropoda:



Pulmonata: Planorbidae) was collected. We found this small planorbid on wood and macrophyte substrates in the littoral zone. Prior to our collection, *G. deflectus* had been reported from North Carolina only from Greenfield Lake, New Hanover County (Adams 1990), although Lenat (1983) reported an unidentified *Gyraulus* sp. from Cane Creek, Orange County, that could be this species.

We encountered *Musculium securis* (Prime, 1852) (Bivalvia: Veneroida: Sphaeriidae) only in a narrow drainage ditch of a small pond in Wilson County, where it occurred in loose sediment among macrophytes. Adams et al. (1990) list *M. securis* as Undetermined status. Previously, Herrington (1962) reported this clam's geographic distribution to include North Carolina, and Dawley (1965) examined specimens from Guilford County, North Carolina.

*Pisidium variable* (Prime, 1851) was collected from Cattail Creek at SR 1738 in Johnston County, the first report of this peaclam in North Carolina. Previously, this species was considered to have a northern distribution, with Virginia and Tennessee being its most southern limit (Herrington 1962, Heard 1963).

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Morphometric Variation Between  
*Bufo woodhousii fowleri* Hinckley (Anura: Bufonidae)  
on Assateague Island, Virginia and  
the Adjacent Mainland

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**ABSTRACT**—Mark and recapture studies of *Bufo woodhousii fowleri* in 1988 and 1989 on Assateague Island, Virginia, and the adjacent mainland showed that adult toads were significantly ( $P \leq 0.05$ ) more abundant on the island than the mainland in both years. The masses and snout-vent lengths (SVL) of toads were significantly greater on the mainland than on the island in both years, and adults were significantly larger at each location in 1989 than in 1988. Sex ratios were close to 1:1 or 1:2 on the island and the mainland in both years. Male and female toads were not sexually dimorphic in size at either location in 1988 or 1989. The smaller of two adult size classes on the island in 1988 was not present on the island in 1989; there were three size classes on the mainland in both years. Electrophoretic analysis revealed the low genetic diversity of the two populations. There were no noteworthy differences in allele frequencies or polymorphism ( $P = 0.142$ ) and mean heterozygosity ( $\hat{H} = 0.01$  island;  $\hat{H} = 0.03$  mainland) between the two populations.

This study documents morphometric differences that often exist between island and mainland populations. Factors that could affect the inverse relationship between toad abundance and size include low genetic diversity at loci controlling body size, the age structure of each deme, and intraspecific competition or physiological stress on the island. These explanations for small body size of island toads are consistent with the existing hypotheses of small immigrant size, small food particle or food supply, and age structure of populations that are presented to account for the smaller size of island versus mainland conspecifics.

Differences in size between island and mainland conspecifics include gigantism and dwarfism, but explanations and correlations for differences in size structure of such populations are difficult to determine (Carlquist 1974). On Atlantic coast barrier islands, slider turtles (*Chrysemys scripta*) are larger on Kiawah and Caper's is-

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lands than natural populations on the adjacent mainland, and Gibbons et al. (1979) attributed this disparity in size to higher quality diets and warmer temperatures on the islands. The eastern hognose snake (*Heterodon platyrhinos*) is smaller on Assateague Island, Virginia, than on the adjacent mainland (Edgren 1961, Scott 1986). The basis for the smaller *H. platyrhinos* size on Assateague Island compared to the size of animals on the mainland is not known.

In typical amphibians, the effects of mainland versus island ecology on amphibian biology are more difficult to predict because environmental factors might differentially affect the aquatic and terrestrial phases of the life cycle. We studied the size and abundance of *Bufo woodhousii fowleri* in three different habitats on Assateague Island compared with a population in three different habitats on the adjacent Delmarva peninsula.

### MATERIALS AND METHODS

We captured *Bufo woodhousii fowleri* in drift fences and pitfall traps (Gibbons and Semlitch 1981) randomly placed in three habitats on the island (146.78 ha) and mainland (30.45 ha) study areas. There was one replicate for drift fences and pitfall traps in each habitat at each location in 1988 and one replicate for each location in 1989. Upon capture, toads were measured (SVL, mm), weighed (g), sexed, toe clipped (Clarke 1972) and released. Recaptured toads were measured and weighed before release, but the sizes of recaptured toads are not presented because periods between recapture events were too brief to accurately assess growth in either toad population.

In 1988, toads were trapped in coniferous forests, meadows, and primary dunes on Assateague Island (37°56'N; 75°20'W) from 2 to 29 June and in deciduous forests, coniferous forests, and meadows on the adjacent mainland (37°56'N; 75°29'W) from 2 to 16 July. We stopped trapping on the mainland when it was apparent that about 50% of the population in the area was marked (Davis 1982). In 1989, toads were trapped concurrently from 10 June to 10 July in coniferous forests and meadows on the island, and in deciduous and coniferous forests on the mainland. The Schnabel method (Schnabel 1938, Smith 1980) was used to estimate the mean abundance of toads in habitats at each location. The assumptions inherent in mark-release-recapture studies, constant population size and random samples (Schnabel 1938), were met because we could detect recruitment, represented by juveniles, and because the placement of drift fences and pitfall traps at each location was random.

Abundance and sex ratios were analyzed with the Systat™ ANOVA procedure. Adult SVL and mass were analyzed with a



2X3 nested ANOVA. Juvenile SVL was analyzed with a one-way ANOVA. We used Tukey's *w*-test (Steel and Torrie 1980) to compare mean toad SVL and mass for each year and location. Size frequency distributions were tested with probit analysis (Harding 1949). The level of accepted significance was 95% ( $P \leq 0.05$ ).

Horizontal starch (12%) gel electrophoresis was performed on muscle in toe clips taken from 25 toads at each location ( $N = 50$ ) on 30 April and 23 May 1989. Muscle from toe clips was homogenized in 200  $\mu$ L of ice cold buffer and centrifuged at 10,000 g for 10 minutes. Proteins were originally separated using four buffers of different pH and composition (0.1445 M tris, 0.0471 M citrate, TC, pH 7.0; 0.0100 M tris, 0.0100 M maleate, 0.0013 M EDTA, 0.0010  $\text{MgCl}_2$ , TM, pH 7.4; 0.0884 M N-3-aminopropylmorpholine, 0.0399 M citrate, AC, pH, 7.0; 0.0300 M lithium hydroxide, 0.1126 M boric oxide, LiOH A, pH 8.2; 0.0503 M tris, 0.0080 M citrate, LiOH B, pH 8.7) to determine the system best suited to identify enzyme polymorphisms. Buffers were those described by Selander and Yang (1969) and Clayton and Tretiak (1972). The following enzymes (EC number, locus abbreviation, buffer) were resolved from prepared homogenates: lactate dehydrogenase (1.1.1.27, *Ldh*, TC), malate dehydrogenase (1.1.1.37, *Mdh*, TC), phosphoglucose mutase (5.4.2.2, *Pgm* TC), peptidase 3.4.-.-, Ap, LiOH). Proteins were separated over 14 hours at 165 V for TC gels and 180 V for LiOH gels. Protein assays were modified from methods described by Shaw and Prasad (1970) and Harris and Hopkinson (1976). Allele frequency, deviation from Hardy-Weinberg equilibrium, polymorphism, single locus heterozygosity ( $H$ ), and mean heterozygosity ( $H$ ) were calculated from the seven loci resolved (Hartl 1988, Smith 1989). A locus was considered to be polymorphic if the frequency of the most common allele was less than 0.99.

## RESULTS

Two hundred forty-one adult toads were captured in 1988, and 139 adult toads were captured in 1989. The high percentage of recaptures (60.0%) for mainland toads in 1988 (Table 1) precipitated the termination of the study on the mainland because individuals were consistently recaptured after only 9 days of mark and release. This suggested that the mainland population was adequately sampled to describe the status of the toads in the study area even though less time was allocated for trapping toads on the mainland. Trapping rates in 1988 support this assumption. Trapping rates (number of individuals per day  $\pm 1$  SE) were significantly greater for the island ( $11.9 \pm 2.5$ ) than the mainland ( $1.4 \pm 0.5$ ).

Table 1. Abundance, snout-vent length (SVL), mass and sex ratios of *Bufo woodhousii fowleri* on Assateague Island, Virginia and the adjacent mainland; *n* represents the total number of individuals in the sample (excluding recaptures), and *r* equals the number of recaptures.

Year	Location	<i>n</i>	<i>(r)</i>	SVL (mm)				Mass (g)			
				Abundance		M		F		M	
				$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1988	Island	226	(33)	303	101	38.3	0.5a <sup>1</sup>	37.6	0.6a	7.8	0.2a
1988	Mainland	15	(9)	6	2	48.2	2.5b	49.8	3.3b	14.7	2.1b
1989	Island	111	(21)	116	46	44.6	0.5c	43.2	0.6c	12.5	0.3c
1989	Mainland	28	(12)	4	2	57.2	1.2d	59.8	4.2d	22.5	1.4d
										29.9	5.2d
										11.4	0.4c
										14.8	3.0b
										7.6	0.3a
											1:1.7
											1:0.6
											1:0.8
											1:1.5

<sup>1</sup>Values followed by the same letters are not significantly different (Tukey's *w*-test,  $\alpha = 0.05$ ).



Toads were significantly more abundant on the island than on the mainland in both years. We captured *Bufo woodhousii fowleri* in all habitats at each location except primary dunes on the island and meadows on the mainland. Although habitat had no significant effect on toad abundance in areas where toads were captured, toads in deciduous and coniferous forests made up a large portion of the mainland sample in 1988 (82.2%, 17.8%) and in 1989 (75.7%, 24.3%). Toads in coniferous forests and meadows made up a large portion of the island sample in 1988 (67.4%, 32.6%) and in 1989 (81.5%, 18.5%). Sex ratios close to 1:2 in 1988 ( $\chi^2 = 1.049$ ,  $P > 0.25$ ) and 1:1 in 1989 ( $\chi^2 = 0.26$ ,  $P > 0.50$ ) on the island (Table 1) and close to 1:1 in 1988 ( $\chi^2 = 0.600$ ,  $P > 0.25$ ) and 1:2 in 1989 ( $\chi^2 = 0.318$ ,  $P > 0.50$ ) on the mainland were observed.

The mean snout-vent lengths (SVL) and masses of *B. w. fowleri* were significantly larger in 1989 than 1988 at both locations (island-15.1%, 53.0% and the mainland-18.1%, 66.8%). However, mainland toads were significantly larger than island toads in both years (Table 1). Male and female toads were not sexually dimorphic in size at either location (Table 1).

We observed size classes, detected by probit analysis, of 25-45 and 46-57 mm SVL on the island in 1988 (Fig. 1); whereas two juvenile size classes (18-20 and 21-35 mm), which represent recruitment from the previous year in forest and meadow habitats, and one adult size class (36-57 mm) were observed in 1989.

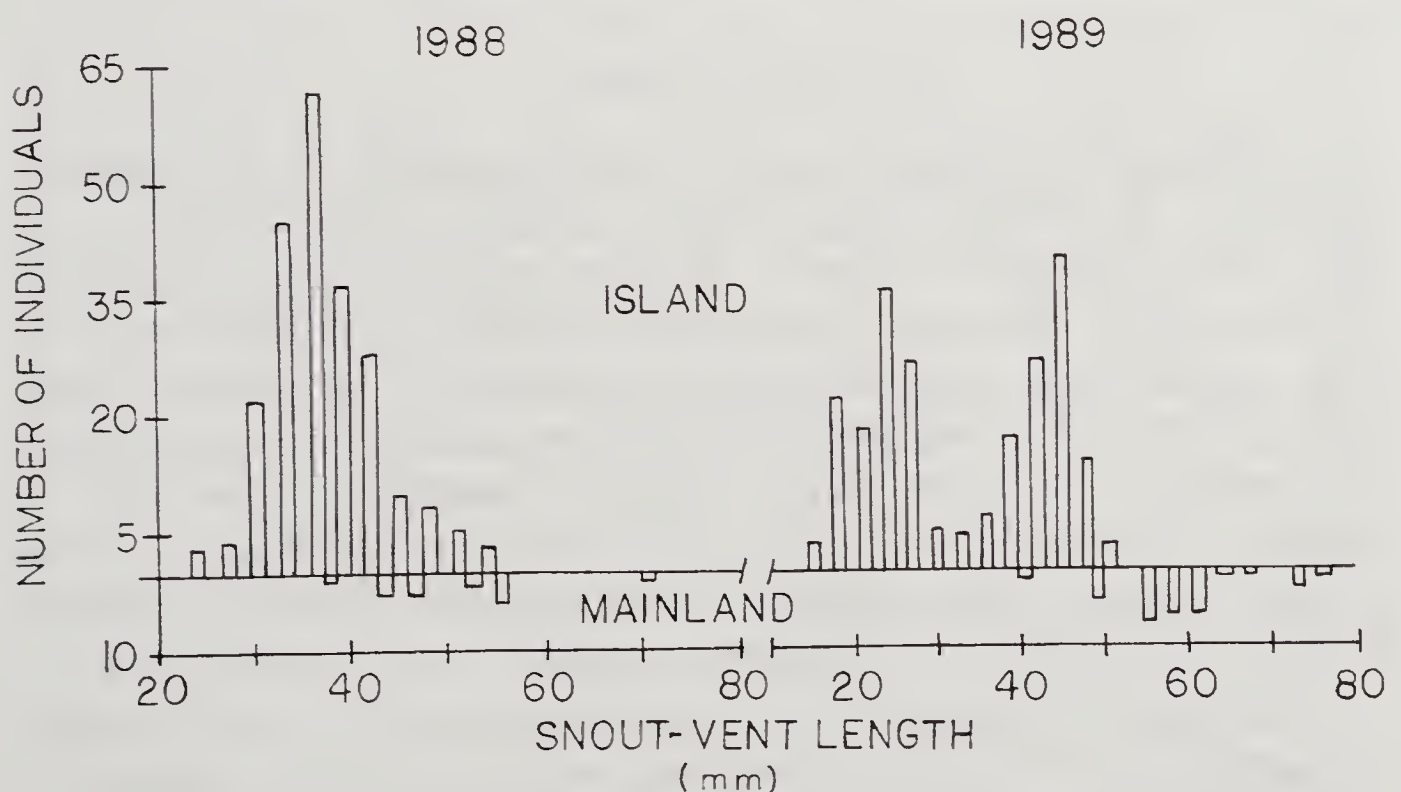


Fig. 1. Size frequency distributions of *Bufo woodhousii fowleri* collected in pitfall traps in 1988 and 1989 on Assateague Island (above the x-axis) and the adjacent mainland (below the x-axis).

mean size of the largest size class on the island decreased from 1988 to 1989, and the smaller of the two size classes observed in 1988 was not observed in 1989. Three size classes were observed on the mainland in 1988 (38-42, 45-48, and 52-57 mm) and in 1989 (39-50, 54-62, and 66-76 mm) (Fig. 1).

There were no juveniles on the island in 1988 or on the mainland in either year. Of the 111 juveniles captured on Assateague Island in 1989, 40 were from coniferous forests, and 71 were from meadows. Forest juveniles ( $25.8 \pm 0.5$  mm SVL) were significantly ( $P \leq 0.05$ ) larger than meadow juveniles ( $23.5 \pm 0.4$  mm SVL).

Genetic diversity was low at each location, and there were no noteworthy differences in allele frequencies between the island and mainland toad populations at the seven loci studied. Six of seven enzyme loci (*Ap*, *Ldh-4*, *Ldh-5*, *Mdh-2*, *Pgm-1*, and *Pgm-2*) were monomorphic in both populations. *Mdh-1* had two alleles, MDH-1<sup>100</sup> and MDH-1<sup>105</sup>, in each population. The frequency of MDH-1<sup>100</sup> was 0.96 on the island and 0.12 on the mainland, and the frequency of MDH-1<sup>105</sup> was 0.04 on the island and 0.88 on the mainland. Polymorphism (*P*) for toads at both locations was 0.142. Heterozygosity (*H*) for MDH-1 was 0.08 on the island and 0.12 on the mainland. Mean heterozygosity (*H*) was 0.01 for island toads and 0.03 for mainland toads. Deviations from Hardy-Weinberg expectations at the *Mdh-1* locus were not significant in the island ( $\chi^2 = 0.0434$ ,  $P \leq 0.01$ , 1 df) or mainland ( $\chi^2 = 1.469$ ,  $P \leq 0.01$ , 1 df) samples.

## DISCUSSION

Differences between the size structure of island and mainland populations of animals (Edgren 1961, Carlquist 1974, Gibbons et al. 1979, Scott 1986) and between adjacent mainland toad populations (Oldham 1985) are not unusual. Our results show differences in body size between toads of Assateague Island and the adjacent mainland, providing an example of an insular population of amphibians with smaller body sizes than mainland conspecifics. However, the differences between the island and mainland populations of toads occurred within a narrow window of time in which mainland samples of toads were small; thus, further comparative study is required.

Reasons for smaller body sizes of island animals are reviewed by Carlquist (1974). Small immigrants might be more successful at colonizing an island, smaller body size might be in response to selective predator pressures, or small body size might be an adaptation to smaller food objects or food supplies. Although the eastern



hognose snake (*Heterodon platyrhinos* Latreille) is a major predator of toads and is abundant on the island (Scott 1986), we found only one hognose snake while trapping on the island. In the absence of any predator-prey data, it is not possible to assess whether predator pressures on toad body size exist. We suggest other explanations for the smaller body size and greater abundance of island than mainland toads. Two of these are consistent with the hypotheses of Carlquist (1974), whereas a third hypothesis is consistent with the discussion of age structure of King (1989).

The island and mainland toad populations have very similar genetic composition with respect to each other and low genetic diversity compared to other populations of this species (Green 1984, Breden 1988). The considerable genetic similarity of the two populations is not entirely surprising. First, Assateague Island likely was colonized from the north as sand from currents was deposited on remnants of Pleistocene barriers (Leatherman 1979). Second, gene flow likely occurred between the two populations for the 200 or more years that existed between the time that Assateague Island assumed its current formation during colonial times and 1933, when a hurricane produced the inlet that exists today between Assateague Island and the part of the peninsula known as Fenwick Island (Leatherman 1979, Amos 1980). The low genetic variation exhibited in these two populations of toads could be attributed to a combination of biological (e.g., inbreeding, fidelity to breeding sites) and historical factors (e.g., founder's effects, post-Pleistocene changes in sea level which restricted gene flow to the narrow window of land at the northern end of the peninsula). Although no genetic variation was detected at each of seven loci studied in the island and mainland populations of Virginia, except *Mdh-1*, considerable genetic variation is present at five of these seven loci in toads from east-central Mississippi (J. M. Hranitz and W. J. Diehl, Mississippi State University, personal observation). Therefore, from the preliminary genetic analysis we present, further study of the genetic composition of the island and Delmarva toad populations and toad populations on the mainland proper, using a larger sample of individuals as well as enzyme loci, is warranted.

If body size is a quantitative genetic character, then the low genetic diversity of a population restricts the body size of individuals in the deme to only a small proportion of the total distribution of body size in the species. If the seven loci studied serve as genetic markers for the loci controlling body size, then the small body size of toads on Assateague Island might result from low genetic diversity at loci controlling body size. Low genetic

diversity could be caused by genetic bottlenecks, most likely due to founder's effects, such as only small immigrants colonizing the island (Carlquist 1974) as might occur simply by chance or because smaller body size confers an energetic or cryptic advantage during dispersal. This hypothesis can also explain why larger island than mainland conspecifics are observed in other instances.

An inverse relationship between size and abundance of toads on the mainland and the island could occur if the growth of toads on the island was stunted while "ecological release" (Soule 1966) permitted the species to be abundant in response to the depauperate herpetofauna of Assateague Island (Lee 1972). Size frequency distributions of toads at each location in both years suggest that this is true. Factors that can cause stunting on the island include intraspecific competition, which may be the predominant biotic factor controlling population size considering the depauperate herpetofauna of the island, and physiological stress caused by fluctuating environmental factors (Parsons 1990). The more important factors likely include salinity of impoundments, availability of water on the island, and quality of habitats at each location. Intraspecific competition and physiological stress are consistent with the food supply hypothesis (Carlquist 1974) because each involves a limiting environmental factor that either favors or produces individuals with small body size.

The island and mainland demes could have different age structures, with mainland toads being older and larger, and island toads being younger and smaller. The lack of sexual dimorphism and the overall increase in mean body size in each deme from 1988 to 1989 is similar to growth of young cohorts of *B. calamita* (Boomsma and Arntzen 1985). These results suggest that both demes are composed of young toads, although the demes might not be the same age or have the same proportion of toads from different cohorts. This concept is not consistent with any of the ideas of Carlquist (1974) but is consistent with an explanation for body size variation in *Thamnophis sirtalis* and *Nerodia sipedon* in the Lake Erie area (King 1989).

Studies reporting differences between island and mainland conspecifics often attribute differences between populations to unique features of islands (Carlquist 1974, Gibbons et al. 1979). In some cases, differences between island and mainland populations could, in fact, be artifacts of sampling two distinct populations, an opportunity that does not always present itself in continuous or adjacent mainland populations. Studies by Oldham (1985) and King (1989)



suggest this is true. Body sizes of mainland *T. sirtalis* and *N. sipedon* varied as much as, and in some cases more than, island versus mainland conspecifics. Variation in abundance and size between mainland toads in adjacent agricultural habitats (Oldham 1985) was similar to our results for island versus mainland *B. w. fowleri*.

Assuming that similar-aged juveniles are involved, the differences in SVL between juveniles from coniferous versus meadow habitats probably reflect an expression of the modifying factors early in ontogeny: faster growth rates for tadpoles in impoundments surrounded by forest habitat, faster growth rates for juveniles in forest habitats, or migration of juveniles from meadow habitats to coniferous forest habitats. An indication of greater abundance of toads in wooded versus meadow habitats on Assateague Island and the capture of toads only in wooded habitat on the mainland indicate that adult *B. w. fowleri* prefer woodland habitat (see Lee 1972). Woodland habitat likely plays an important role in the life history of *B. w. fowleri* on Assateague Island. Other investigations of herpetofaunal colonization patterns of Atlantic Coast barrier islands indicate that it is not island size but the amount of woodland habitat that is most highly correlated with numbers of reptile and amphibian species present (Gibbons and Coker 1978).

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Leatherback Turtle, *Dermochelys coriacea*  
(Reptilia: Dermochelidae): Notes on Near-shore  
Feeding Behavior and Association with Cobia

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**ABSTRACT**—Leatherback turtles (*Dermochelys coriacea*) were regularly seen 250 m off North Topsail Beach, North Carolina, during May and early June 1990 and 1991, in close association with and feeding on *Stomolophus meleagris* jellyfish. Cobia (*Rachycentron canadum*) occurred in close proximity to the turtles.

Lee and Palmer (1981) summarized the near-shore occurrence of leatherback turtles in the waters of North Carolina. Even though leatherbacks are perhaps the most pelagic of all sea turtles (Ernst and Barbour 1972, Bustard 1973), Lee and Palmer (1981) encountered most turtles in the shallow waters over the continental shelf, well away from the beach. Ernst and Gilroy (1979) reported that this turtle remains close to shore during migrations and is seasonally common along the coast from Virginia to New Jersey.

Because little is known about leatherback behavior and distribution, we report observations on feeding behavior, fish associations, and two strandings at North Topsail Beach, Onslow County, North Carolina.

## METHODS

Observations were made nearly daily from Salty's Pier at North Topsail Beach, North Carolina, during May and June 1990 and 1991. D.F. was employed by the pier and fished near the distal end of the pier during his off-time. G.S.G. searched for turtles from the pier on 12-15 occasions during this time interval. Informal

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discussions with fishermen on the pier helped document the temporal pattern of leatherbacks in the area. Salty's Pier extends 250 m from the beach.

## RESULTS

G.S.G. saw leatherbacks from Salty's Pier on 19 May 1990 (0740 hours), 13 May 1991 (1600 hours), and another larger individual on 13 May 1991 (1638–1640 hours). D.F. witnessed leatherbacks nearly daily while he was employed at the pier from May to mid-June 1991. The largest leatherback was estimated to be about 2-m long. Pier fishermen reported seeing these turtles several times a day on some occasions; the turtles passed within 10 m of the end of the pier. Water depth where most sightings occurred was about 4 m, and ocean surface temperatures recorded daily at North Topsail Beach during May and early June 1990 ranged from 16 to 24C.

Sightings of leatherback turtles seemed to correspond with cabbagehead or cannonball jellyfish (*Stomolophus meleagris*). These jellyfish were so abundant at Salty's Pier during May and early June 1990 and 1991 that 50–200 could be seen daily. These jellyfish were about 20 cm in diameter, moved vertically in the water column, and most remained in close proximity to the pier. D.F. observed leatherbacks eating several cabbagehead jellyfish in May and June 1991 off Salty's Pier.

C. Rader (pier employee, personal communication) reported watching a leatherback about 1.7-m long ingest 50–80 cabbageheads in spring 1991 at Myrtle Beach, South Carolina. From his fishing pier vantage point, Rader was able to observe feeding behavior at close range. He reported that just before ingesting a jellyfish, the turtle appeared to blow out air and water through its nose and mouth before consuming the entire jellyfish. No jellyfish or leatherbacks were seen or reported by fishermen after mid-June 1991.

D.F. and other fishermen saw three to four cobia close to leatherbacks each time a turtle swam by the pier. The cobia ranged in size from 0.6 to 1.3 m and typically maintained positions either slightly above or below the swimming turtle.

Two stranded leatherback turtles on North Topsail Beach were examined and measured during the May to mid-June 1990 and 1991 observation period. One decomposing turtle without obvious external injuries washed up at Salty's Pier on 16 May 1990. It was about 150-cm long. The second decomposing turtle washed up 5 km south of Salty's Pier on 24 May 1991. It measured 162 cm (curved carapace length) by 90 cm (curved carapace width). Both were docu-



mented with photographs deposited at the North Carolina State Museum of Natural Sciences, Raleigh.

## DISCUSSION

Perhaps in some years leatherback turtles congregate with *Stomolophus* jellyfish along the coastline of Topsail Island, North Carolina, during May and early June. The feeding observation at Myrtle Beach, South Carolina, further suggests that leatherbacks could appear whenever cabbagehead jellyfish appear in abundance along the Carolina coast.

Further searches for turtles from the ends of fishing piers should be conducted elsewhere along the Southeast coast to document peaks of occurrence. *Stomolophus meleagris* occurs from Cape Hatteras, North Carolina, to Brazil (Schwartz 1979) and is found in North Carolina from May to November. It enters sounds and waterways when salinities are similar to that of the ocean (Schwartz 1979). One large leatherback encountered in the Neuse River near New Bern, North Carolina, on 16 November 1975 (Schwartz 1977, Lee and Palmer 1981) might not be atypical if it was associated with its jellyfish prey. Leary (1957) reported numerous leatherbacks within a dense school of *Stomolophus meleagris* off the Texas coast on 17 December 1956.

Stomach analyses have shown that leatherback turtles feed primarily on medusae, siphonophores, and salpae (Bleakney 1965, Eckert et al. 1989). Direct feeding observations include accounts of adults feeding on *Aurelia* off the coast of Washington State (Eisenberg and Frazier 1983) and on *Rhizostoma octopus* off Great Britain (Penhallurick 1991). Morgan (1989) and Penhallurick (1991) reported leatherbacks associating with *Rhizostoma pulmo*, *R. octopus*, *Cyanea* sp., and *Chrysaora isocetes* jellyfish off Great Britain. Collard (1990) reported seven leatherbacks in areas of maximum abundance of jellyfish and other gelatinous forms in the eastern Gulf of Mexico, and Lazell (1980) linked leatherback movements with the abundance of *Cyanea* sp. jellyfish off New England.

Eckert et al. (1989) and Eckert (1992) hypothesized that the daily diving patterns of leatherbacks are closely related to the abundance of jellyfish and other zooplankton in the deep scattering layer. For example, shallow dives would be more likely during the night when the jellyfish were closer to the surface, and deeper dives would be more likely during daylight when the prey could be 300 m or more deep.

On several occasions the leatherbacks passed close to live bait fishing rigs (mackerel rigs) at Salty's Pier and did not attempt to

eat the tethered bluefish (*Pomatomus saltatrix*), spots (*Leiostomus xanthurus*), or menhaden (*Brevoortia tyrannus*).

Cobia are known to swim in proximity to sea turtles, sharks, and large rays (Manooch and Raver 1984). We do not know if the cobia benefit from this association by scavenging on food scraps or by gaining hydrodynamic advantages. Cobia tend to be found most commonly around sea buoys and other floating shelters (Robins et al. 1986). Perhaps the association of cobia with swimming leatherbacks is simply the result of cobia seeking their preferred habitat. Penhallurick (1991) reported remoras (*Remora remora*) and pilot fish (*Naucrates ductor*) swimming alongside leatherback turtles off Great Britain.

### CONCLUSIONS

Leatherback turtles were observed feeding on cabbagehead jellyfish at North Topsail Beach, North Carolina during May and early June 1990 and 1991. Jellyfish populations were high, and the turtles might be following the jellyfish bloom northward during this period. Leatherback turtles should be looked for whenever jellyfish populations are high. The association of cobia with the swimming leatherbacks also warrants further study.

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# Additional Evidence for the Specific Status of *Nerodia cyclopion* and *Nerodia floridana* (Reptilia: Colubridae)

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**ABSTRACT**—Preserved specimens were used in a morphological comparison of *Nerodia cyclopion* and *N. floridana*. Data included counts of head and body scales and body scutes as well as measurements of head scale dimensions. Comparisons of these data revealed significant differences in the numbers of ventral scutes, subcaudal scutes, and dorsal scale rows. Discriminant analysis of head scale measurements proved to be a reliable tool separating these taxa and revealed no evidence of gene exchange. I concur with the recent elevation of the two taxa to full species; the two species are at least parapatric in the western Florida Panhandle.

Two subspecies of the green water snake, *Nerodia cyclopion* (Duméril, Bibron, and Duméril, 1854) have been recognized since the description of *N. c. floridana* by Goff (1936). Goff (1936) documented that, on the basis of ventral coloration, numbers of ventral and subcaudal scutes, numbers of infralabial scales, and relative tail lengths, the eastern form (*N. c. floridana*) could clearly be separated from the western form (*N. c. cyclopion*). Goff (1936) speculated that intergrades between *Nerodia c. cyclopion* and *N. c. floridana* would be found somewhere between Mobile, Alabama, and Leon County, in the Florida Panhandle. He had no specimens from this area, however, and so had no direct evidence for distributional contact or intergradation.

Serological and immunoelectrophoretic comparisons within the genus *Nerodia* led Pearson (1966:8) to comment that “a low relationship between *N. c. cyclopion* and *N. c. floridana* indicates that a re-evaluation of their status as subspecies should be considered; elevation to full species is suggested.” Mount (1975:208) cited localities for both *cyclopion* and *floridana* from Baldwin County, Alabama, and stated that “clear evidence of intergradation . . . is lacking,” although he noted that specimens from extreme southeastern Baldwin County appeared to be intermediate on the basis of ventral coloration. Lawson (1987) reported the results of molecular studies of the New World natricines, in which he proposed specific

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status for the two forms. Conant and Collins (1991) followed this suggestion and treated the two taxa as separate species.

In this article I present the results of a morphological comparison of *Nerodia cyclopion* and *N. floridana* and report previously unpublished collection localities for green water snakes in western Florida.

## MATERIAL AND METHODS

I examined 381 preserved specimens of green water snakes. Complete data (head, body, and tail length; scale counts; and head scale measurements) were obtained from 217 specimens. Fewer data (usually head, body, and tail lengths, and scale counts) were recorded for the remaining ones.

Snout-vent length and tail length (for specimens with complete tails) were measured to the nearest millimeter with a 1-m rule. Head length was measured with dividers and a 10-cm rule to the nearest millimeter from the tip of the rostral scale to the posteriormost point of the mandible.

Ventral scutes were counted by the method of Dowling (1951). Subcaudal counts did not include the terminal scale. Dorsal row counts were made one head length posterior to the head, at midbody, and one head length anterior to the vent. Meristic data on head scalation included the number of suboculars, preoculars, postoculars, temporals, supralabials, and infralabials. Student's *t*-test of equivalency of sample means was used to determine if any of these characters were useful in separating the two taxa. Relative tail length was found to decrease ontogenetically, and thus was treated by regression analysis.

Certain head scales were measured to quantify head shape (Fig. 1). These dimensions were determined to the nearest 0.01 mm with a dissecting microscope fitted with an ocular micrometer. For discriminant analysis of this mensural data, I used release 2.1 of the Statistical Package for the Social Sciences (SPSS), available through the Louisiana State University Systems Computing Center. For the discriminant analysis of head scale data, the raw measurements were separated into two groups. One group, termed the holdout group, contained data derived from 49 specimens of both taxa (46 *cyclopion*, 3 *floridana*) from Alabama and the Florida panhandle. This group, then contained those specimens most likely to possess intermediate character states if gene flow is occurring between the two taxa. The second group, termed the calibration group, contained data from all remaining specimens: 90 *cyclopion* and 78 *floridana*.



The first phase of the analysis tested the calibration group with stepwise discriminant analysis. The best discriminating variables varied by sex, so in all analyses the sexes were treated separately. All head scale measurements were entered into the analysis program; those characters which did not contribute significantly to the discrimination of the two taxa were discarded. The program, using these data, then assigned each specimen to a species group (*cyclopion* or *floridana*) and calculated the probability of error in this assignment. The second phase then tested the specimens in the holdout group using the parameters established with the calibration group data.

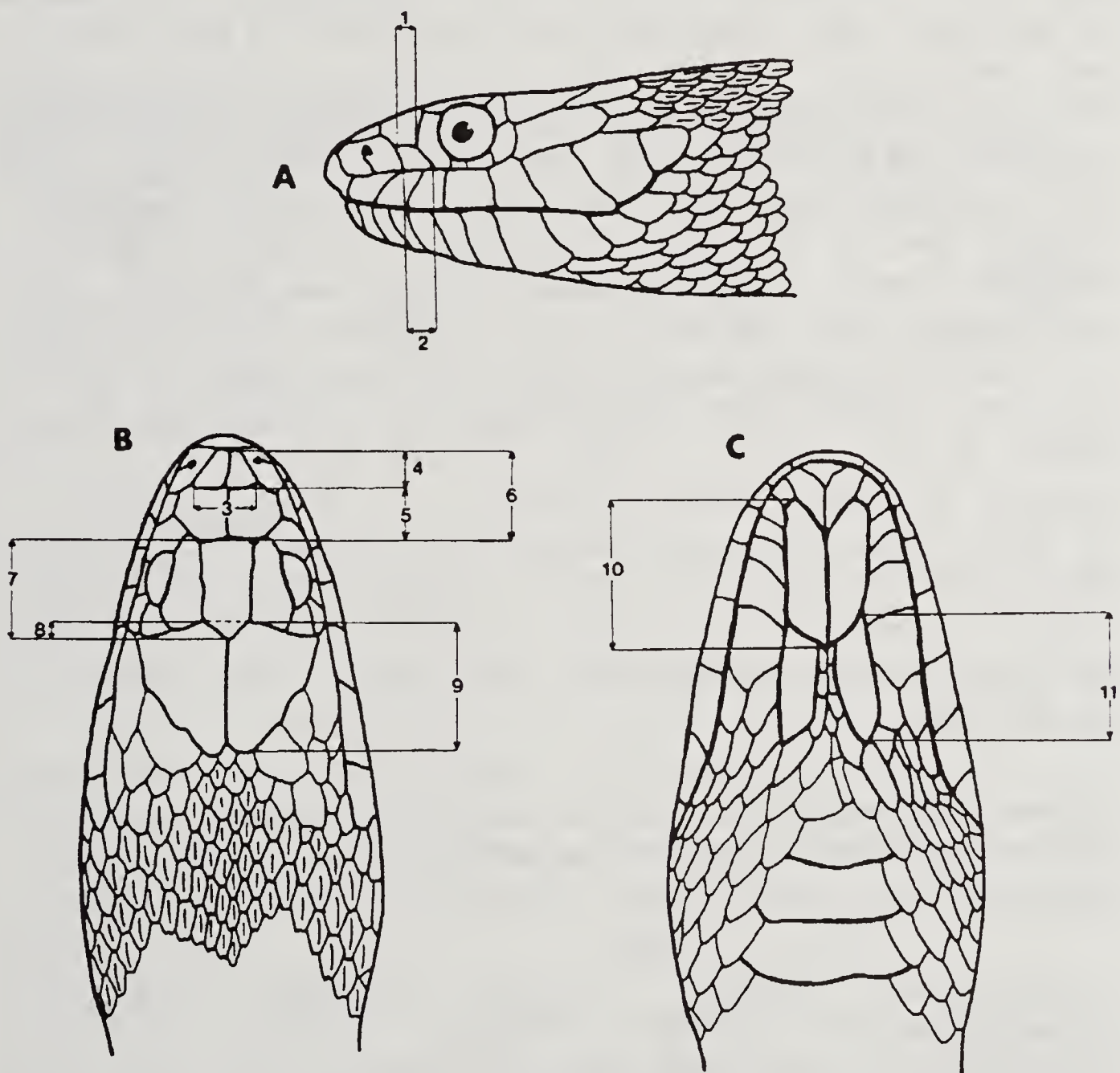


Fig. 1. Views of the head of *Nerodia cyclopion* illustrating the method of measurement of head scales. The characters are (1) loreal dorsal length (LD), (2) loreal ventral length (LV), (3) muzzle width (MW), (4) internasal length (IL), (5) prefrontal length (PF), (6) muzzle length (ML), (7) frontal length (FL), (8) frontal extension length (EL), (9) parietal length (PL), (10) anterior genial length (AG), and (11) posterior genial length (PG).

RESULTS

SCALATION

Mean numbers of preocular, postocular, subocular, supralabial, infralabial, and temporal scales do not distinguish *N. cyclopion* from *N. floridana*. Regression analysis revealed no significant difference between the two taxa in relative tail length.

Ventral scute counts do not appear to be related to a significant degree to either sexual dimorphism or geographic variation. However, the mean number of ventrals for *cyclopion* ( $\bar{x}$  = 141.6, range = 133–145,  $n$  = 249) is significantly higher than that of *floridana* ( $\bar{x}$  = 136, range = 129–141,  $n$  = 130,  $P$  < 0.01). As in most species of snakes, there is sexual dimorphism in the number of subcaudal scales. This difference is significant in both *cyclopion* and *floridana* ( $P$  < 0.01); males of both taxa have 5–11 more subcaudals than females from the same localities. In both sexes *cyclopion* has fewer subcaudals than *floridana*. In *cyclopion*, northern populations have fewer subcaudals than southern populations, whereas there is no discernible geographic variation in *floridana*. Subcaudal counts in *floridana* show no significant geographic variation. Samples from the vicinity of the presumed zone of parapatry are significantly different ( $P$  < 0.01). The mean subcaudal number for male *cyclopion* from southern Alabama and Escambia County, Florida, is 73.9 (range = 70–76,  $n$  = 8), whereas that of male *floridana* from the western panhandle is 77.5 (range = 77–78,  $n$  = 2). Mean values for female *cyclopion* and *floridana* from the same areas are 66.7 (range = 61–69,  $n$  = 15) and 70 ( $n$  = 1), respectively. The ranges of these values for the two taxa do not overlap, and the differences are significant even with the small sample sizes for *floridana*.

Table 1. Most frequent dorsal scale row formulae for *Nerodia cyclopion* and *N. floridana*. See Sanderson (1983) for complete scale row data.

Dorsal scale rows (anterior-midbody- posterior)	Males				Females			
	<i>cyclopion</i>		<i>floridana</i>		<i>cyclopion</i>		<i>floridana</i>	
	% of		% of		% of		% of	
	Number	sample	Number	sample	Number	sample	Number	sample
25-23-19	15	31.3	0	0	0	0	0	0
27-25-21	33	68.8	15	34.1	57	70.4	0	0
29-25-21	0	0	15	34.1	10	12.3	11	22.9
29-27-21	0	0	11	25.0	12	14.8	15	31.3
29-27-23	0	0	3	6.8	2	2.5	22	45.8



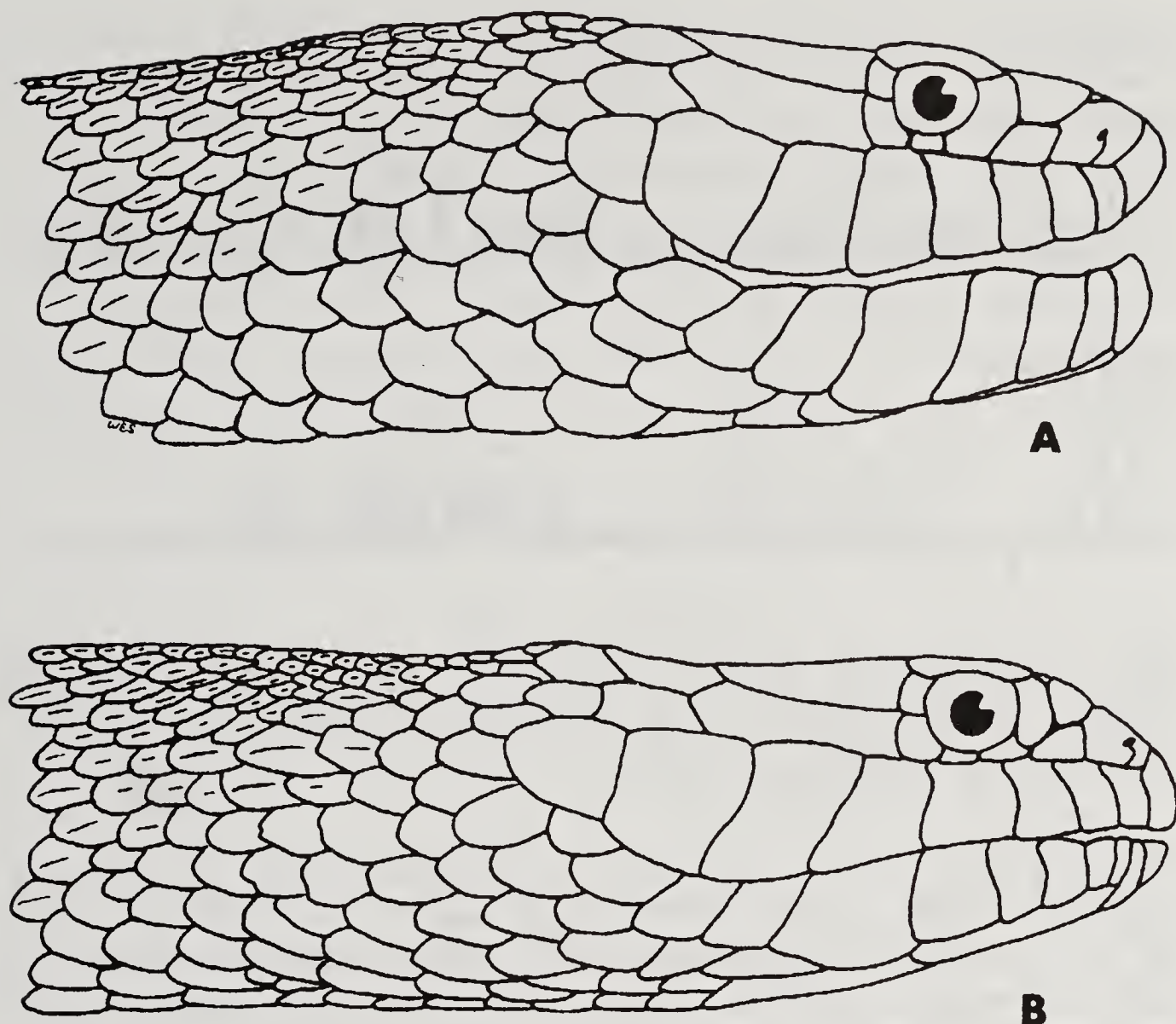


Fig. 2. Typical head profiles of large adult *Nerodia cyclopion* (A) and *N. floridana* (B). Bar = 20 mm.

There are no discernible patterns of geographic variation in the number of dorsal scale rows in either taxa. Significant sexual dimorphism occurs, with females typically having two rows more than conspecific males. The two taxa are separable on the basis of sample means ( $P < 0.01$ ). Abbreviated dorsal scale row data are summarized in Table 1, and complete scale row data are in Sanderson (1983).

#### HEAD SCALE MEASUREMENTS

The head shape of *cyclopion* is distinctly different from that of *floridana*, particularly in the region of the snout. This difference is not pronounced in juveniles and small adults, but is conspicuous in larger individuals (Fig. 2). Particularly noteworthy is the abruptly sloped snout of *floridana*. Also, the head of *floridana* is narrower in dorsal view, being more laterally compressed than that of *cyclopion*.

Discriminant analysis of the head scale data from the calibration group indicated that the two taxa are distinct groups, with an

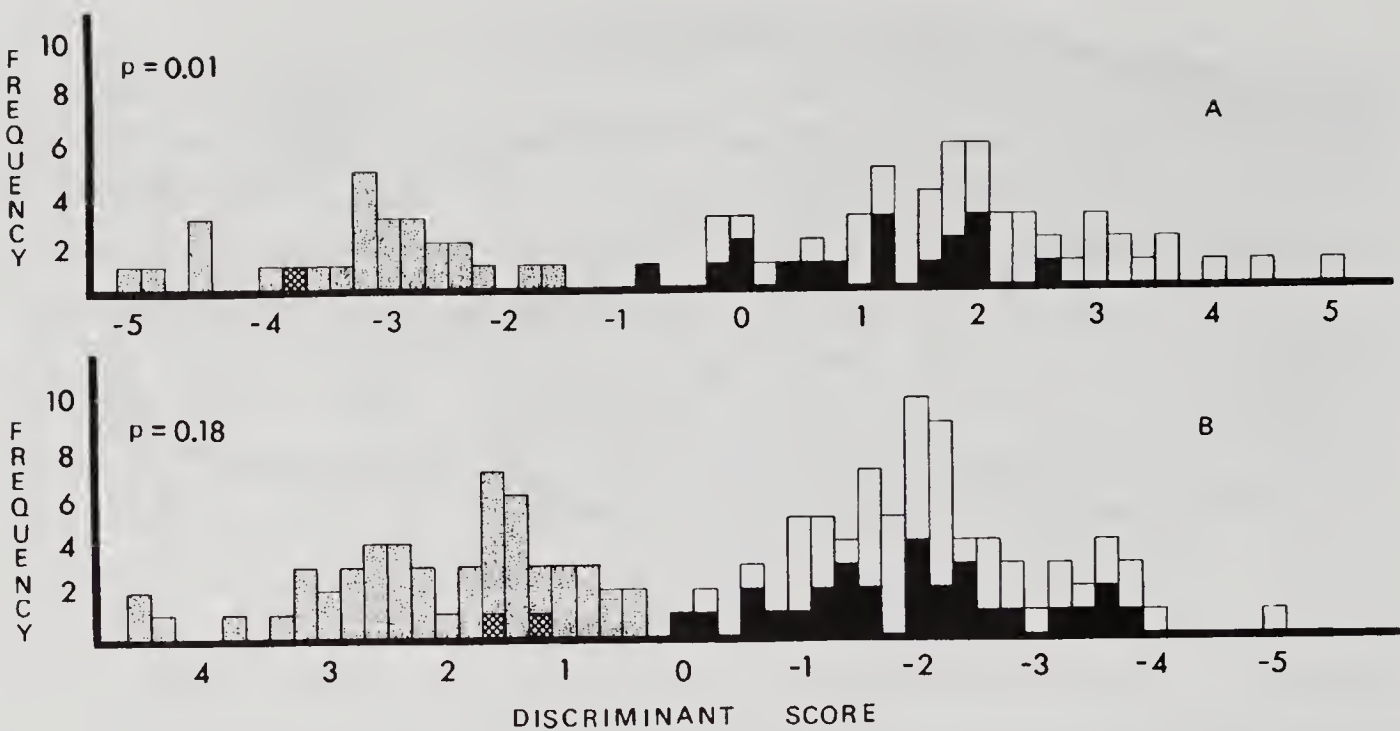


Fig. 3. Histograms of discriminant scores for male (A) and female (B) *Nerodia cyclopion* calibration sample (open bars), *N. cyclopion* holdout sample (shaded bars), *N. floridana* calibration sample (stippled bars), and *N. floridana* holdout sample (crosshatched bars).

extremely high level of confidence ( $P < 0.0001$ ) (Fig. 3). Internasal length, prefrontal length, muzzle length, and frontal extension length did not contribute significantly to the discrimination in either sex and were dropped from the analysis. The remaining variables (loreal dorsal length, frontal length, muzzle width, posterior genial length, loreal ventral length, anterior genial length, and parietal length) and their standardized discriminant function coefficients are given in Table 2. For both taxa, 100% of the specimens were classified correctly by the discriminant analysis, meaning that all specimens, which had been previously categorized as either *cyclopion* or *floridana* based

Table 2. Variables incorporated by the stepwise discriminant analysis, listed in order of entrance, with standardized discriminant function coefficients. See Figure 1 for description of variables.

Males		Females	
Variable	Function	Variable	Function
LD	0.581	FL	2.335
FL	-1.561	MW	-2.736
MW	2.666	PG	1.150
PG	-0.922	LD	-0.587
LV	-0.797	LV	0.916
AG	0.972	AG	-0.985
PL	-0.843		



on ventral coloration and scale counts, fell within the predicted group based on head scale data alone.

I tested the holdout group against the classification criteria established in the calibration group analysis. Again, 100% of the males of both taxa were classified correctly. All female *floridana* were also correctly classified, but two female *cyclopion* were misclassified as *floridana*. The first, (Auburn University Museum 22559, Alabama: Baldwin County, 6 miles NNW town of Stockton, Douglas Lake) has a typical *cyclopion* ventral color pattern. Its dorsal scale row formula (27-25-21) resembles that found in 70.4% of the female *cyclopion* I examined. This dorsal scale formula was found in none of the female *floridana*. The snout of this individual is somewhat shorter and narrower than is typical for *cyclopion*, and this feature caused the discriminant analysis to classify it as *floridana*. However, variation from the normal *cyclopion* pattern is slight; this individual was identified as *floridana* with an estimated 50.2% probability of being correct. Considering all the data available, as well as its geographic location, I conclude that this individual is a *cyclopion*.

The second misclassification (University of South Alabama 1930, Alabama: Baldwin County, Negro Lake) also has typical *cyclopion* ventral coloration and dorsal scale row counts (27-25-21). It is the longest specimen of *cyclopion* I examined (1,035-mm snout-vent length, 1,322-mm total length), which exceeds by 52 mm the record for *cyclopion* as listed by Conant and Collins (1991). The muzzle width is less than that of other *cyclopion* of similar length, which may be an allometric consequence of its large size. This variation probably exceeded the bounds of the classification criteria, which were established with data from smaller specimens. Again, the data suggest that this animal is also a *cyclopion*.

If gene flow has occurred between the two taxa in the zone of contact, the distributions of the discriminant functions of the holdout groups would be skewed away from those of the calibration groups. This was tested (for *cyclopion* only due to the small sample sizes in *floridana*) by comparing sample means of the discriminant functions of the groups with *t*-tests. No significant difference in sample means was found in female *cyclopion* ( $P = 0.183$ ,  $t = 1.34$ ,  $df = 76$ ), but in the male population the scores of the holdout group did appear skewed away from the distribution of the calibration group scores. In addition, the *t*-test indicated a significant difference between the two groups ( $P = 0.012$ ,  $t = 2.61$ ,  $df = 56$ ). An obvious explanation for these contradictory data is not apparent. Since gene exchange, if present, must affect both sexes, I suggest that the relatively small sample size for male *cyclopion*

could have resulted in artificially dissimilar values. The distributions of the female *cyclopion* groups, with somewhat larger sample sizes, were not significantly different. Further, the distributions of the discriminant scores of the two taxa do not overlap (Fig. 3). I conclude there is a lack of gene flow between parapatric populations of *cyclopion* and *floridana*. Continued investigation, ideally with additional specimens of *floridana* from this critical area, is definitely warranted.

#### DISTRIBUTION

Fieldwork undertaken to clarify the distribution of green water snakes in western Florida was largely unsuccessful. Collecting trips to this area produced no specimens of *N. floridana* and only one *N. cyclopion* (Louisiana State University Museum of Zoology 40401, Florida: Escambia County, Perdido Bay Golf Club). Another *cyclopion* from the same locality (LSUMZ 40402) was procured for me by a local collector. The presence of this population in Escambia County indicates that *N. cyclopion* should be considered a resident of the state of Florida, although Ashton and Ashton (1981) did not include *cyclopion* in their work on the snakes of Florida.

Carr (1940) reported *Nerodia cyclopion cyclopion* from Leon County, Florida. These specimens could not be located and are presumed lost, and Carr was not certain that they were *cyclopion* (P. Meylan, University of Florida, personal communication). The westernmost specimen of *floridana* (AUM 6087, Florida: Escambia County, Perdido River at Seminole) has an atypically dark venter when compared with specimens from the Florida peninsula. However, scale data identify it as *floridana* with a very high level of confidence ( $P = 0.999$ ). The green water snake remains unknown from Santa Rosa and Okaloosa counties, Florida, although a specimen clearly referable to *floridana* was taken in Walton County near the Okaloosa-Walton County boundary. Given the specimens presently available, it appears that the distributions of *cyclopion* and *floridana* are adjacent or overlapping in Escambia County, Florida (Fig. 4).

#### DISCUSSION

Specimens intermediate between *Nerodia cyclopion* and *N. floridana* have been reported twice from southern Alabama. Mount (1975) reported a population of green water snakes in extreme southeastern Baldwin County that he considered to be intermediate on the basis of ventral coloration. Although some of these animals do have venters that are somewhat lighter than *cyclopion* from more inland parts of Baldwin County, they are very similar to specimens from other Gulf coastal regions, especially those from coastal Mississippi and



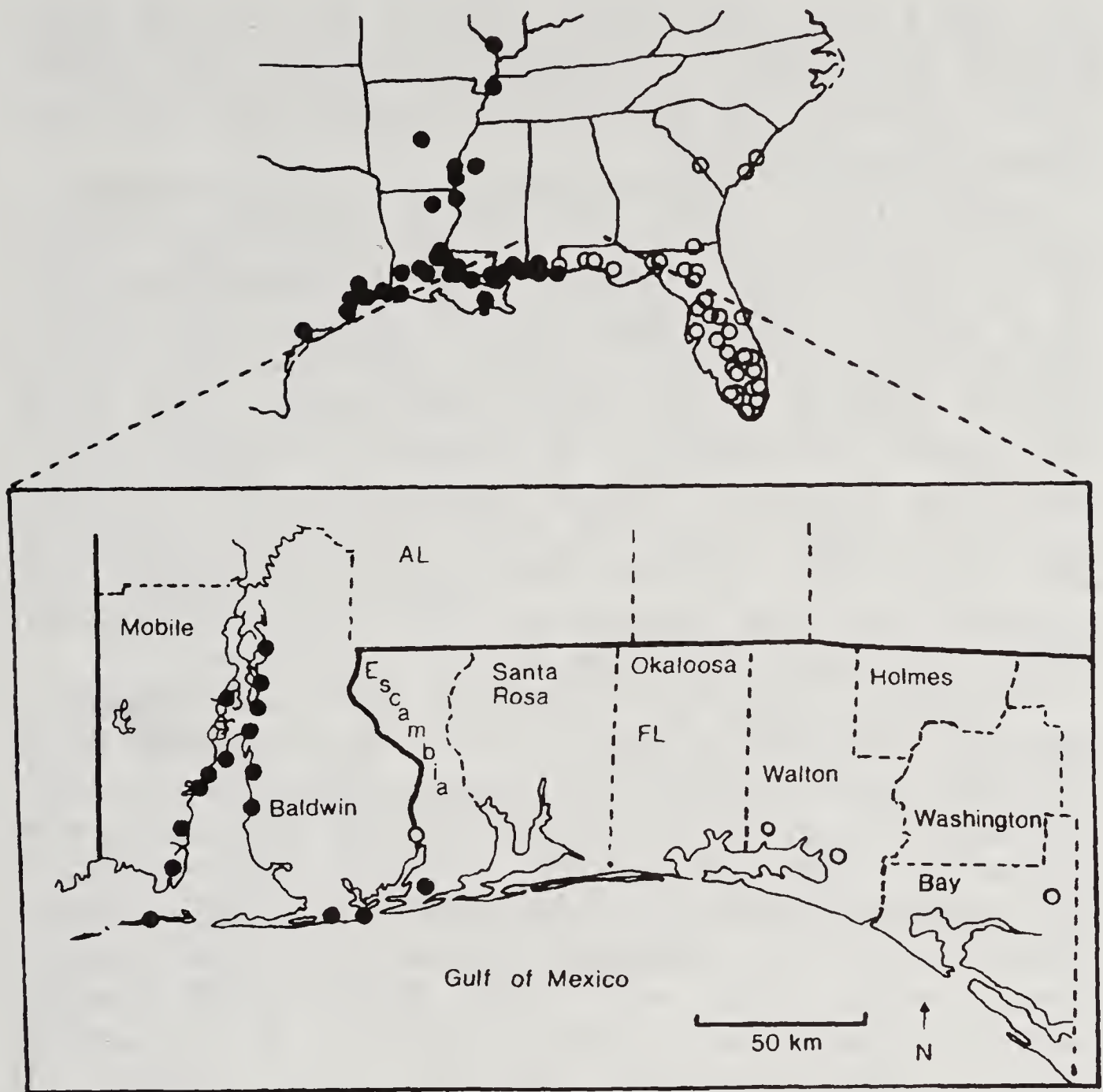


Fig. 4. Known localities for *Nerodia cyclopion* (solid circles) and *N. floridana* (open circles) in southern Alabama and western Florida. The inset map shows localities of specimens examined in this study (most circles represent more than one specimen).

Dauphin Island, Alabama. This lightened coloration may be a result of selective pressures present in a coastal environment rather than an indication of gene exchange between *cyclopion* and *floridana*. On the basis of scale characters, these individuals are all clearly identifiable as *cyclopion*.

Mount (1975) also mentions specimens of *floridana* taken along the eastern shore of Mobile Bay. These specimens (LSUMZ 15780, Alabama: Baldwin County, Mobile Bay 3.95 miles west of Spanish Fort; Auburn University Museum 3030, Alabama: Baldwin County, west of Fairhope) are classified as *cyclopion* by body and head scale analysis, but both are nearly amelanistic, with extremely light ventral and dorsal color patterns. One of these (AUM 3030) has

also suffered from extreme fading after preservation. Scallation clearly identifies both animals as *cyclopion*. Another specimen (LSUMZ 15779) collected at the same time as LSUMZ 15780 has typical *cyclopion* ventral coloration.

Cooper (1977) reported collecting an intergrade specimen in extreme southern Baldwin County, Alabama. This specimen was lost (W. E. Cooper, Auburn University, personal communication), but Cooper provided a second snake from this locality (LSUMZ 40089, Alabama: Baldwin County, Gulf Shores State Park, Lake Shelby) which he said has a ventral color pattern similar to that of the first specimen. In scalation, it is referable to *cyclopion*, but the ventral color is atypical in that the crescentic areas, which normally are cream to white in color, are nearly obliterated by blotches of dark pigment. I have seen two other specimens with similar atypical patterns, both from Louisiana, and thus do not believe this coloration to be indicative of intergradation.

Although *cyclopion* and *floridana* have not been collected together, the two forms do appear to be at least parapatric in the area along the Perdido River, the Alabama–Florida state boundary. My analysis reveals no clear evidence of gene exchange between the two taxa. Additionally, the work of other researchers has revealed significant biochemical differences between the two taxa. Pearson (1966) reported a “low relationship” between the taxa and suggested elevation to full species. More recently, Lawson (1987) employed starch-gel electrophoresis to assay 35 gene loci of *Thamnophiine* snakes and found fixed allelic differences between *cyclopion* and *floridana* at seven of these loci. He concluded that *cyclopion* and *floridana* are sister species, with the degree of separation being somewhat greater than that which separates *Nerodia rhombifera* and *N. taxispilota*. In light of this body of evidence, I concur with Lawson and support his proposal that *Nerodia c. cyclopion* and *N. c. floridana* be elevated to monotypic species, *Nerodia cyclopion* and *Nerodia floridana*, respectively.

#### SPECIMENS EXAMINED

*Nerodia cyclopion*—Alabama: AUM 3030, 19345–46, 22105, 22290, 22448–52, 22455–59, 25970, 26618, 29371. CMNH 67353–55, 67385–86. LSUMZ 15779–80, 40089. MCZ 318. MMNS (AR)2424(A–C). NMNH 56259. UAHC 51–546, 53–14. UF 50399. USA 757, 1801, 1929–32, 2074–76, 2127, 2194, 2227. Arkansas: UF 48036. NMNH 56258. Florida: LSUMZ 40401–2. Illinois: INHS 8749, 10002. LSUMZ 7543. NMNH 1639. Louisiana: LSUMZ 1566, 2839–43, 2846–47, 2937, 4785, 8205–06, 10466, 12071, 12933, 12985, 13135–36, 13556,



13701–02, 13767–68, 13780–81, 13795, 14394, 16933, 17320, 17669, 18286, 18669, 18761–62, 20180, 20276, 20282–83, 20314, 20338–39, 20340–41, 20703, 20722, 20729, 20734, 21059, 22557, 22953, 23179–80, 23305, 23531, 24081–84, 24086, 24093, 24521, 24669, 34308, 40285, 40296, 40329. MMNS AR-2427. TU 12830–31, 12836, 12860–61, 12863–66, 12872, 12914, 12965, 12995–96, 12998–99, 13000, 13040. UAHC 53–14, 53–42. Mississippi: AMNH 46751. CMNH 5248–49. MCZ 149576. MMNS (AR)2423, 2425, 2426(A–C), 2431 (A–B), 2433–37. NMNH 103179. UAHC 65–3517, 65–3518. Missouri: CMNH 7165. NMNH 24466, 35654, 56256–57. Tennessee: NMNH 10397–98. UIMNH 2159–60. Texas: AMNH 67626–27, 67891–92. CMNH 827, 829, 1216, 1221, 1238, 1240, 1242, 1244, 1246–50, 1254, 1258, 1260–63, 60261. INHS 3135. TCWC 3250, 14755, 18213, 27425–28, 27432–34, 33806–08, 33811, 46555–56. UF 4386–87. UIMNH 1137–42, 1362–63.

*Nerodia floridana*—Alabama: AUM 6087. Florida: ChM CR2285. LSUMZ 40399, 40400. UAHC 53–36. UF 2127, 2286, 2370–72, 2491, 2809, 2858, 3913, 4712, 4758–59, 4762, 4766, 4779, 4850, 4883, 7125, 7217, 7286, 7511, 7869(1–2), 8800, 14211, 14498, 16126–27, 17386, 18136, 18348, 21367, 21467, 45766–71, 45778–79, 45781–83, 45789, 45790–92, 45804, 45806, 45808, 45858, 45860, 47859, 50366–67, 50369, 50372, 50374, 50377–78, 50388–89. Georgia: CMNH 33497. NMNH 130115–16. South Carolina: ChM (CR)2270, 2272, 2281–82, 2284. SREL 91, 739, 2223.

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# Observations on Crayfish Predation by Water Snakes, *Nerodia* (Reptilia: Colubridae)

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**ABSTRACT**—Field observations of ingestion of crayfish are reported for the colubrid snake *Nerodia cyclopion*. We surmise that the presence of crayfish in the gut contents of water snakes might not be attributable solely to secondary ingestion of other food items. Crayfish seem to be of minor importance in the diet of water snakes, but patterns of use of this food resource are still poorly understood. Future studies should indicate the size and degree of digestion of crayfish so that a determination of primary or secondary ingestion can be made.

Water snakes of the genus *Nerodia* generally prey on fish and frogs (Mushinsky 1987), unlike the closely related crayfish specialists in the genus *Regina*. However, the importance of other prey items is unclear. The significance of crayfish in the diets of fishes, amphibians, and reptiles has been addressed by Penn (1950) and Neill (1951). Penn (1950) noted that crayfish were important in the diet of *Nerodia erythrogaster*, but this conclusion was based on examination of only one specimen. Based on observations of recently captured *N. sipedon* disgorging crayfishes, Neill (1951) reported that *N. rhombifer* and *N. sipedon* also included crayfish in their diets.

Most of the literature concerning the predation of crayfish by water snakes is based on examination of stomach contents and not on field observations of actual ingestion. Neill and Allen (1956) argued that care must be taken in analyzing feeding habits of snakes so as not to discount the possibility of secondary ingestion (obtaining prey items from the gut of the primary prey species) of food items. They suggested that crayfish fragments found in the stomachs of *N. erythrogaster* and *N. sipedon* might represent the stomach contents of fishes ingested by snakes. The chitinous exoskeleton of crayfish might be more resistant to digestion than the tissues of primary vertebrate prey, and therefore, the exoskeleton will persist

in the predator's stomach. This has been documented in crocodilians (Jackson et al. 1974, Garnett 1985), but evidence in snakes is lacking. The objectives of our paper are to provide data concerning field observations on the ingestion of crayfish by the green water snake (*N. cyclopion*) and to discuss the importance of crayfish in the diet of water snakes.

### STUDY AREA AND METHODS

Observations of foraging snakes were made along Alligator Bayou, Ascension Parish, Louisiana. Alligator Bayou is in a swamp formerly subjected to backwater flooding from the Mississippi River. Elevated areas in the swamp are dominated by bottomland hardwoods (*Quercus* spp., *Ulmus* spp., *Celtis laevigata*, and *Liquidambar styraciflua*). Lower areas are dominated by *Taxodium distichum*, *Nyssa sylvatica*, *N. aquatica*, and *Cephalanthus occidentalis*.

A 14-foot boat equipped with an outboard motor was used to search for snakes along waterways and canals. At night, a Q-beam<sup>R</sup> spotlight (250,000 candle power) was used to observe snakes. The stomach contents of snakes collected for a parasitological study were examined, and prey items were identified to the lowest possible taxon (Fontenot 1990).

Crayfish are abundant at this site and are harvested commercially for human consumption. According to Huner (1975), red swamp crayfish (*Procambarus clarki*) are most abundant during elevated water levels in the spring, when they mate. As water levels decline in the summer, the crayfish burrow down to the water level and remain below ground until water levels rise again in the late winter and early spring.

### RESULTS

One male *N. cyclopion* (SVL = 50.1 cm, BM = 123.3 g) was observed foraging in relatively clear water at 2241 hours on 30 May 1989. This snake slowly moved its head from side to side, while holding its jaws slightly agape in the characteristic foraging posture described for water snakes by Mushinsky (1987). The snake made contact with and immediately seized a red swamp crayfish, *Procambarus clarki*, (carapace length = 25.0 mm, total length = 48.3 mm). The crayfish was molting; consequently, it did not possess a hardened exoskeleton. The snake twisted its head and body during prey capture, positioned the crayfish in its mouth, and then ingested the prey tail-first within 30 seconds of capture. This position was later verified when the snake was dissected. Several unidentified small fish were also present in the gut contents. Both the



specimen of *N. cyclopion* and the crayfish have been deposited in the Clemson University Vertebrate Museum (CUSC#931).

Examination of 60 *N. cyclopion* from this locality revealed that one other snake contained crayfish in its gut. Additionally, 3 of 29 *N. fasciata* and 1 of 24 *N. rhombifer* examined from the same locality contained crayfish remains (Fontenot 1990).

## DISCUSSION

Conant and Collins (1991) listed frogs, salamanders, fish, and crayfish as food items for members of the genus *Nerodia*. However, chemical preference studies of newborn water snakes have shown that crayfish are not a preferred food item (Burghardt 1968, Mushinsky and Lotz 1980). Crayfish have been reported as prey items for adult *N. cyclopion* (Kofron 1978), *N. erythrogaster* (Clark 1949), *N. fasciata* (Mushinsky and Hebrard 1977), *N. rhombifer* (Minton 1944, Sisk and McCoy 1964, Bowers 1966, Kofron 1978), and *N. sipedon* (Zelnick 1966, Fraker 1970, Camp et al. 1980), which suggests crayfish consumption might be restricted to larger individuals. In all cases except for *N. erythrogaster* (Clark 1949), crayfish were infrequent prey items. Brown (1958) concluded that the importance of crayfish in the diet of water snakes has been unintentionally exaggerated. He found no crayfish in 207 stomachs of *N. sipedon* he examined even though crayfish were abundant at his study site. Crabs, another crustacean, have been reported to be ingested by *N. clarki* (Mount 1975).

Although some crayfish remains could be attributed to secondary ingestion, in many instances it is likely that crayfish are consumed as a primary prey item. Because molting crayfish lack a digestive-resistant chitinous exoskeleton, they are probably consumed more frequently than food habits studies indicate. We suggest that in future studies the size and degree of digestion (intact crayfish or fragments) be noted to help determine if crayfish are primarily or secondarily ingested.

Based on our limited observations and a review of the literature, we believe that crayfish do not comprise a large portion of the diets of most species of water snakes; however, crayfish might be consumed directly by water snakes. Differential digestion rates of vertebrate and crayfish prey might introduce bias in analysis of reptile food habits (Jackson et al. 1974, Garnett 1985). Patterns of use of this food resource by water snakes may be subject to ontogenetic shifts and seasonal or regional differences in foraging ecology.

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Food and Feeding Behavior of Adult Snowy Grouper,  
*Epinephelus niveatus* (Valenciennes) (Pisces: Serranidae),  
Collected off the Central North Carolina Coast with  
Ecological Notes on Major Food Groups

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**ABSTRACT**—Food items from snowy grouper (*Epinephelus niveatus*) (Valenciennes) were collected on 30 commercial handline fishing trips off central North Carolina from March 1985 through April 1986 in waters 146–228-m deep. More than 5,000 snowy grouper stomachs were examined, but fewer than 5% contained food. Embolism prevented the frequent extraction of intact digestive tracts. Snowy grouper fed on crustaceans (72% by volume), fish (18%), and mollusks (10%). Crabs, primarily *Portunus spinicarpus* (Stimpson), accounted for approximately 90% of the food items and 72% of the volume. Most foods were inhabitants of bottom or near-bottom waters and were small enough to be swallowed whole. Ecological notes are included on major food groups. Competition for food between *E. niveatus* and other serranids is believed to be minimal because only a few other groupers were caught. Of the other groupers, the yellowedge grouper (*E. flavolimbatus* Poey) contained foods most similar to those consumed by snowy grouper. Compared with other sympatric species, *E. niveatus* fed on foods most similar to red porgy (*Pagrus pagrus*).

Reef fish and macroinvertebrate assemblages on the outer continental shelf edge and upper slope of central North Carolina at depths between 140 and 240 m have received little scientific attention. This is in spite of steadily increasing commercial hook-and-line activity in that depth range throughout the Carolinas since 1979

(Low and Ulrich 1983). At these depths energy flow, trophic structure, species competition for space and food, and the extent of substrate use by deep reef associated predators remain poorly known (Duke University Marine Laboratory 1982).

The snowy grouper, a tertiary predator, is the dominant grouper at depths greater than 140 m off the Carolinas (Low and Ulrich 1983, Chester et al. 1984). In 1984 the snowy grouper was by mass the most important reef fish caught commercially along the central North Carolina coast (eastern Onslow and Raleigh bays) (Epperly and Rhode 1985). That year an estimated 34,771 *E. niveatus* totaling 162,112 kg were harvested statewide. The species represented 14.0% by mass of all reef species commercially caught by bottom longline, handline, and fish traps.

Adult snow grouper are consistently found in deeper water, whereas juveniles dominate the shallow end of the depth range. In part this may reflect years of intensive fishing pressure in 40–120-m intermediate depths and only relatively recent pressure beyond 183 m off central North Carolina where the largest adults were encountered. The shift toward larger grouper with increasing depth, which has been noted by Low and Ulrich (1983) in South Carolina and by Moore and Labisky (1984) in the lower Florida Keys, might also indicate movement of grouper into deeper water with the onset of maturity.

Inaccessibility of adult snowy grouper at depths beyond 140 m has restricted life history data collection in the South Atlantic Bight to limited exploratory cruise data or materials available from dock-side sampling (Low and Ulrich 1983, Matheson and Huntsman 1984, Epperly and Rhode 1985). Typical of other biological aspects of *E. niveatus*, little is known of its feeding habits. From 1972 to 1981 the National Marine Fisheries Service (NMFS) Beaufort, North Carolina, attempted to collect snowy grouper stomach samples from recreational headboats operating between Cape Hatteras and Cape Romain and from research vessels (Matheson 1981; G. Huntsman, National Marine Fisheries Service, Beaufort, personal communication). In a live bottom study conducted on the outer continental shelf off North Carolina for the Minerals Management Service, Bureau of Land Management (BLM), Duke University Marine Laboratory (1982) also collected snowy grouper food items, as did the South Carolina Wildlife and Marine Resources Department (1982) in a similar BLM study off South Carolina and Georgia.

Results of all three efforts were discouraging. Of hundreds of grouper stomach examined by NMFS (R. Matheson III, Apex High School, Apex, North Carolina, personal communication) only 131



were recovered intact. Eighteen contained food, represented by decapod crustaceans (78% of number; 72% of volume) and unidentified fish (20% of total prey number; 28% of volume). Identifiable food items included one Spanish lobster (*Scyllarus depressus*) (Smith) and brachyuran crabs: *Acanthocarpus alexandri* Stimpson, *Calappa angusta* Milne Edwards, *Calappa flammea* (Herbst), *Iliacantha subglobosa* Stimpson, *Ovalipes stephensoni* Williams, and *Portunus spinicarpus* (Stimpson) (Duke University Marine Laboratory 1982, South Carolina Wildlife Marine Resources Department and Duke University Marine Laboratory 1982, Parrish 1987). Food items were collected primarily from the outer shelf in summer from headboats operating in 37–110 m (R. Matheson III, personal communication). The North Carolina BLM effort produced only 14 intact stomachs, two of which contained food (Duke University Marine Laboratory 1982). The South Carolina and Georgia BLM outer shelf project obtained no snowy grouper stomachs with food (South Carolina Wildlife Marine Resources Department 1982).

The only other *E. niveatus* feeding study conducted in the southeastern United States was an analysis of intestinal tracts of 26 snowy grouper from the lower Florida Keys (Bielsa 1982). Specimens were collected from May through October at 123–256 m. Fish, primarily pelagic species, dominated (43% of prey number; 47% of total volume). Cephalopods ranked second in numerical importance (21%), although brachyuran crabs were second in volumetric importance (32%).

Problems associated with sampling snowy grouper for food items include fish availability, condition of the fish at dockside, and stomach eversion resulting from embolism. Adult snowy grouper are uncommon in trawl catches (Bullis and Thompson 1965, Barans and Burrell 1976, Keiser 1976, Cupka et al. 1977), and hook-and-line sampling on small, patch reefs from large research vessels has proven expensive, labor intensive, and ineffective in providing sufficient samples for food analysis (R. Matheson III, personal communication; C. Manooch III, personal observation). Snowy grouper with intact stomachs are rarely brought to commercial docks because groupers normally are gutted and iced at sea. Ungutted snowy grouper caught by headboat anglers do reach the dock. However, they are not abundant and are now caught almost exclusively in waters less than 100 m where few large fish are found. Visual observations of snowy grouper feeding behavior have been limited to a single submersible observation of individuals near a reef in 125–137 m off North Carolina (Parker and Ross 1986).

Epibenthic predators, particularly those associated with deep water reefs, often feed on small cryptic fish and macroinvertebrates. These prey are ineffectively sampled by trawls, dredges, grabs, and remote cameras. Thus, analysis of snowy grouper stomachs provides additional life history and distribution data on prey items that might otherwise have gone unsampled by conventional sampling methods.

The objective of our study was to define the role of adult snowy grouper as an epibenthic predator in the trophic structure of the shelf-edge and upper-slope communities off the central coast of North Carolina. By sampling aboard a commercial fishing vessel, we were able to (1) identify foods of snow grouper, (2) evaluate their contribution to the diet numerically and volumetrically, and (3) compare the diet of snowy grouper with those of other seranids and with three important sympatric species.

### METHODS

Thirty, 1–4-day commercial handline fishing trips targeting snowy grouper stocks in deep water were made off North Carolina (Table 1). Stomachs were examined and prey items were collected during fishing operations aboard a 12.5-m vessel, and occasionally aboard a 9.4-m sister vessel, based in Beaufort, North Carolina (Table 1). The primary study area was a narrow zone which began approximately 83 km SSE of Cape Lookout and extended about 44 km to the northeast along the outer continental shelf edge and upper-slope crown at depths of 137–194 m. Fishing was conducted from spring through fall. Several spring trips were made to a secondary study area about 57 km south of Cape Hatteras in 168–238 m along the upper slope crown in a 10-km<sup>2</sup> area. In both areas numerous stations, including at least two wrecks, were drift fished with weighted multiple hook rally rigs baited with squid on wire handlines operated from hydraulic reels. A single exploratory longline set in 108 m and a single handline station at 112 m were the shallowest depths fished and contributed fewer than 40 fish to the study.

Bottom topography at 137–194 m typically consisted of scattered rock outcroppings or ledge formations of variable relief and shape which protruded through terrigenous sand substrate of varying coarseness and a variable carbonate shell component. Deeper, particularly in the secondary study area beyond 219 m, a clay-mud substrate was sometimes encountered.

The senior author served full time as a commercial fisherman on the vessels. He cleaned large quantities of fish and recovered food items that would not have been available at dockside. This sampling was an unfunded, volunteer endeavor aboard a vessel whose



primary objective was to catch, clean, and ice as many fish in as short a time as possible. Often only the senior author and the captain were aboard, and there was never more than a second crewman.

When grouper regurgitated food items on deck, it was usually not possible to assign specific items to a particular grouper or to

Table 1. Commercial fishing trips made off North Carolina where snowy grouper digestive tract contents were collected, 1985–86.

Date	Depth (m)	Number of Snowy Grouper	Size (mm TL)	Gutted Mass (kg)	
				$\bar{x}$	Total
2/22/85	194–205	28		14.7	411.6
4/13/85	205–236	44	455–1090	8.8	387.2
4/18–21/85	194	34	450–1070	6.8	231.2
4/26–29/85	111,194–208	157	510–1075	5.3	832.1
5/5/85	196,205	2		8.4	16.8
5/16–17/85	146–155	599	330– 990	2.7	1,617.3
5/21–23/85	146–192	290	330–1010	2.0	580.0
6/2–4/85	155,187–236	150	?–1100	8.1	1,215.0
6/9–11/85	236	58			(394.6) <sup>1</sup>
6/21–24/85	148–155	470		3.3	1,551.0
6/28–29/85	194	223		8.6	1,917.8
7/2–3/85	194	76	435–1030	6.5	494.0
7/9–10/85	146,194	124	410– 990	6.1	756.4
7/14–17/85	108–194	136	390– 990	5.6	761.6
7/20–21/85	194	277	380–1100	8.3	2,299.1
7/30–31/85	194	285	405–1020	4.7	1,339.5
8/5–7/85	143–146	252	404– 990	4.8	1,208.6
8/23/85	194	31		1.8	55.8
8/25–26/85	137–146	184	335– 770	2.9	533.6
8/29–30/85	201–238	85		5.0	425.0
9/3–6/85	141–192	453	?– 980	3.8	1,721.4
9/20–21/85	148	28		1.5	42.0
9/30–10/2/85	148–192	190	405– 860	2.7	513.0
10/19–20/85	159–194	54	515– 850		(158.8) <sup>1</sup>
11/7–8/85	159–194	49		2.2	107.8
11/9–11/85	146–159	178		2.5	445.0
11/19–20/85	146–155	157	335– 785	1.8	282.6
2/19/86	146	1		3.6	3.6
3/16–18/86	141–194	321	350– 876	2.4	770.4
3/25–27/86	146–163	152	365– 760	2.6	395.2
Combined		5,088		4.2	21,370

<sup>1</sup> Estimated gutted mass.

measure individual fish, because sometimes 12–15 grouper would be brought on deck at the same time. Grouper were secured in retaining boxes before gutting. As fish were cleaned, mouths and throats were examined, and boxes were checked for regurgitated prey. Between drifts the deck was scanned for regurgitated foods before rinsing. The senior author examined most grouper caught but gutted only about half, relying on the other crew members to recover food from the remainder.

Catches were predominantly snowy grouper, but other species were occasionally caught (Table 2). If there was any question as to which species regurgitated given items, which was infrequent, the items were not recorded. Regurgitated items less than 15 mm were

Table 2. Additional fish species and numbers captured on hook and line in 141–236 m off central North Carolina during the time frame when snowy grouper were sampled, 1985–86.

Species	Number Caught
Blueline tilefish ( <i>Caulolatilus microps</i> Goode and Bean)	358
Banded rudderfish ( <i>Seriola zonata</i> ) (Mitchell)	90
Vermilion snapper ( <i>Rhomboplites aurorubens</i> ) (Cuvier)	57
Yellowedge grouper ( <i>Epinephelus flavolimbatus</i> ) (Poey)	52
Red porgy ( <i>Pagrus pagrus</i> Linnaeus)	51
Almaco jack ( <i>Seriola rivoliana</i> Valenciennes)	45
Blackbelly rosefish ( <i>Helicolenus dactylopterus</i> ) (Delaroche)	16 <sup>1</sup>
Conger eel ( <i>Conger oceanicus</i> ) (Mitchell)	12 <sup>2</sup>
Greater amberjack ( <i>Seriola dumerili</i> ) (Risso)	6
Spinycheek scorpionfish ( <i>Neomerinthe hemingwayi</i> Fowler)	5 <sup>1</sup>
Reticulate moray ( <i>Muraena retifera</i> Goode and Bean)	4
Scalloped hammerhead shark ( <i>Sphyrna lewini</i> ) (Griffith and Smith)	4
Night shark ( <i>Carcharhinus signatus</i> ) (Poey)	3 <sup>2</sup>
Bignose shark ( <i>Carcharhinus altimus</i> ) (Springer)	2
Tiger shark ( <i>Galeocerdo cuiveri</i> ) (Person and Lesueur)	1
Tilefish ( <i>Lopholatilus chamaeleonticeps</i> Goode and Bean)	1 <sup>1</sup>
Purplemouth moray ( <i>Gymnothorax vicinus</i> ) (Castelnau)	1
Shark toothed moray ( <i>Gymnothorax madierensis</i> )	1
Wreckfish ( <i>Polyprion americanus</i> ) (Schneider)	1
Barrelfish ( <i>Hyperogloyphe periformis</i> ) (Mitchell)	1
Misty grouper ( <i>Epinephelus mystacinus</i> ) (Poey)	1
Speckled hind ( <i>Epinephelus drummondhayi</i> Goode and Bean)	1
<i>Gymnothorax kolpos</i>	1
Total	714

<sup>1</sup> Between Cape Lookout and Hatteras beyond 219 m.

<sup>2</sup> Captured only at dusk or night.



not likely recovered with the same regularity as larger foods. Items positively identified as bait (squid or cut fish) were not saved. Intact stomachs and all loose items were placed in labeled bags on ice. At dockside the unusual food items were photographed, and then all items were preserved in 10% formalin.

In the laboratory prey items were rinsed in fresh water and were identified. Voucher specimens were transferred to 70% alcohol. Decapods were identified from Williams (1984) and were validated by comparison with the Duke University Marine Laboratory reference collection. Stomatopod and decapod voucher specimens were sent to the National Museum of Natural History for identification verification by A. B. Williams and R. B. Manning. Fish were identified with the assistance of S. Ross, North Carolina State University, and G. Burgess, Florida State Museum, Gainesville. Squid were identified from Roper et al. (1984). Food items were identified to the lowest taxon possible, counted, and measured volumetrically by water displacement. Contributions to the diet were calculated as percentage by number and as percentage of volume. Except for the few times when intact stomach samples were obtained, frequency of occurrence could not be determined.

## RESULTS AND DISCUSSION

A total of 5,088 snowy grouper was caught from February 1985 through March 1986. Specimens ranged from 335 to 1,100 mm in total length (TL). Based on the mass-length relationship  $W = 3.6 \times 10^{-8} TL^{2.868}$  (where  $W$  = mass in kg and  $TL$  = total length in mm) (Matheson and Huntsman 1984), masses ranged from 0.6 kg to 19.0 kg (ungutted). We estimate that less than 5% of the snowy grouper boated contained food. Presumably most food items were regurgitated as the fish were brought to the surface. It is also possible that grouper feeding success or effort could have been reduced at specific sites where there were seasonal aggregations of hundreds of grouper. Only 23 fish had contents in uneverted stomachs; other items came from regurgitations on deck or were lodged in throats or gills.

All prey items (fish, squid, and crustaceans) had broad latitudinal distributions and represented a mix of tropical, temperate, and boreal affinities. The southerly flowing Virginian coastal current north of Cape Hatteras presents a cool-water barrier to established adult snowy grouper populations and limits the northerly range of the fish and their crustacean prey with tropical affinities (Cerrame-Vivas and Gray 1966).

## SYNOPSIS OF FOODS

## CRUSTACEA

Snowy grouper fed most extensively on crustaceans. Approximately 91% of the items were crustaceans, representing 73% of the volume (Table 3). Brachyuran crabs dominated this group (90% by number; 72% of the volume) and were represented by 12 species. Other crustaceans were of relatively minor importance and included macruran shrimps, *Solenocera* sp. (probably *S. atlantidis* Burkenroad), and a stomatopod, *Parasquilla coccinea*. The volumetric percentage we recorded for decapods was almost identical to that reported from the earlier NMFS study of snowy grouper from the outer shelf of North Carolina and South Carolina (Duke University Marine Laboratory 1982, Parrish 1987). However, our volumetric percentage for brachyurans was more than twice that noted by Bielsa (1982) for snowy grouper from the lower Florida Keys.

All crustacean prey from snowy grouper have depth ranges extending seaward of 182 m (Williams 1984, Soto 1985). Adult crustaceans are mid-outer shelf or upper slope inhabitants whose bathymetric ranges seasonally overlap (Wenner and Read 1982). Only two crustacean prey, *Ovalipes stephensoni* and *Calappa falmmea*, extend into shallow waters ( $\leq 10$  m). There, seasonal temperature extremes, turbidity, freshwater runoff, light level, and substrate differences present major barriers to most outer-shelf-edge decapods (Cerame-Vivas and Gray 1966, Van Dover and Kirby-Smith 1979, Wenner and Read 1982, Williams 1984).

Although decapod distribution probably remains constant with latitude throughout the South Atlantic Bight (Wenner and Read 1982), bathymetric distribution patterns of prey probably result in major species differences in diet composition between snowy grouper juveniles on the mid shelf and adults on the upper slope. Predator and prey size variations with depth could also be a factor. Commercial hook-and-line captures of juvenile *E. niveatus* have occurred at depths as shallow as 23 m east of the Cape Lookout Shoals "Knuckle" buoy. Juvenile snowy grouper normally are not caught by hook and line until 42–64 m, and usually deeper. Adult snowy grouper have been caught on hook and line as deep as 293–394 m from January through March and as far north as 100 km northeast of Cape Hatteras. Both Cerame-Vivas and Gray (1966) and Wenner and Read (1982) reported only minor overlap of upper slope decapod fauna with inner-shelf species and considered the upper slope crest a major zoogeographical boundary.

Decapod prey of snowy grouper collected at 146–238 m became progressively less common the farther inshore dredging or



Table 3. Items recovered from the digestive tracts of 5,088 snowy grouper caught off North Carolina (less than 5% of the fish were estimated to have contained food), 1985–86.

Item	Number (673)	Percent	Volume (5,442.2mL)	Percent
Crustacea	613	91.08	3,946.3	72.51
Crabs	605	89.90	3,923.3	72.09
<i>Portunus spinicarpus</i>	494	73.40	1,492.3	27.42
<i>Ovalipes stephensoni</i>	19	2.82	584.0	10.73
<i>Cancer irroratus</i>	8	1.19	779.0	14.31
<i>Acanthocarpus alexandri</i>	13	1.93	206.5	3.79
<i>Calappa angusta</i>	44	6.54	434.5	7.98
<i>Cancer borealis</i>	2	0.30	130.0	2.39
<i>Stenocionops spinimana</i>	9	1.34	154.0	2.83
<i>Myropsis quinquespinosus</i>	10	1.49	99.5	1.83
<i>Parthenope pourtelesii</i>	3	0.45	22.0	0.40
<i>Nibilia antilocapra</i>	1	0.15	9.0	0.17
<i>Portunus floridanus</i>	1	0.15	6.5	0.12
<i>Stenorynchus seticornis</i>	1	0.15	6.0	0.11
<i>Solenocera atlantidis</i>	7	1.04	12.0	0.22
<i>Parasquilla coccinea</i>	1	0.15	11.0	0.20
Fish	42	6.24	952.5	17.50
Unidentified remains	22	3.27	341.5	6.27
<i>Peprilus triancanthus</i>	7	1.04	69.0	1.27
Ophichthidae	3	0.45	17.0	0.31
<i>Myrophis punctatus</i>	2	0.30	13.0	0.24
Ophidiidae	1	0.15	5.0	0.09
<i>Macrorhamphosus scolopax</i>	1	0.15	20.0	0.37
<i>Lepophidium jeannae</i>	1	0.15	39.0	0.72
<i>Rhomboplites aurorubens</i>	1	0.15	325.0	5.97
<i>Antigonia capros</i>	1	0.15	83.0	1.53
<i>Hemanthias vivanus</i>	1	0.15	3.0	0.06
<i>Synodus poeyi</i>	1	0.15	4.0	0.07
Congridae	1	0.15	33.0	0.61
Mollusca	16	2.38	536.0	9.85
Gastropoda	1	0.15	4.0	0.07
<i>Conus delessertii</i>	1	0.15	4.0	0.07
Cephalopoda	15	2.23	532.0	9.78
Unidentified squids	10	1.49	37.0	0.68
<i>Loligo pealei</i>	3	0.45	275.0	5.05
<i>Illex illecebrosus</i>	2	0.30	220.0	4.04
Miscellaneous contents	2	0.30	7.5	0.14
Rock fragment	1	0.15	4.0	0.07
Fishing lure skirt	1	0.15	3.5	0.07

trawling was conducted. Of brachyurans recorded in the diet, *Cancer borealis* Stimpson and *C. irroratus* Say rarely leave the upper slope, whereas the following crab species have centers of adult distribution concentrated on the outer shelf or slope crown: *Acanthocarpus alexandri*, *Calappa angusta*, *Iliacantha subglobosa*, *Myropsis quinquespinosa* Stimpson, *Nibilia antilocapra* (Stimpson), and *Stenocionops spinimana* (Rathbun) (Pequegnat 1970, Williams 1984).

*Portunidae*—*Portunus spinicarpus* was the most frequently encountered prey ( $n = 494$ ). We found up to 23 whole *P. spinicarpus* in a single grouper stomach. Also, based on similar states of prey freshness, several grouper had eaten multiple *P. spinicarpus* from the same sites at about the same time. Additionally, snowy grouper fed on both adult and juvenile *P. spinicarpus* of mixed sexes (286 males, 143 females, 65 juvenile or sex undetermined). These had a carapace width (CW) of 21–58 mm. Two gravid females (37 and 42 mm CW, orange and brown eggs, respectively) were recovered from grouper in May 1985, in depths of 146–155 m in the primary study area.

This crab occurred most frequently in gut contents from mid-May through August, declining in importance in fall. We recorded none as prey past mid-October, although winter trawl records were noted from an outer Onslow Bay station (50–100 m) (South Carolina Wildlife Marine Resources Department and Duke University Marine Laboratory 1982) and off Oregon Inlet north of our study area (Musick and McEachran 1972).

The abundance of this crab in the South Atlantic Bight based on trawl efforts parallels this dietary occurrence (Wenner and Read 1982). *P. spinicarpus* was the most common crab and fifth most common decapod collected between 38 and 188 m. Between 111 and 183 m, *P. spinicarpus* represented 16% of the decapod catch.

Ross (1982) reported it to be one of the most important crabs in the diet of the blueline tilefish (*Caulolatilus microps* Goode and Bean), which co-occurs with snowy grouper. We also observed that *P. spinicarpus* was consumed by yellowedge grouper (*E. flavolimbatus* Poey) (present study) and red porgy (Manooch 1977). Two other reef fishes, whitebone porgy (*Calamus leucosteus* Jordan and Gilbert) and vermilion snapper, (*Rhomboplites aurorubens*) (Cuvier) also fed on *P. spinicarpus* in the Carolinas (South Carolina Wildlife Marine Resources Department and Duke University Marine Laboratory 1982).

Rathbun (1930:93), however, made this statement regarding *P.*



*spinicarpus*: "It is worthy to note that whereas this species is abundant in the Florida Keys, no remains were found among the hundreds of fish examined in recent years. This is attributable to the formidable armature of the chelipeds which is sufficient to ward off the enemy." Our observations were that spines on this species and other crustaceans partially penetrated the inner stomach wall.

*Ovalipes stephensoni* was numerically the third most common prey item and was represented by seven males (37–65 mm CW), six females (54–78 m CW), and six specimens of undetermined sex. *O. stephensoni* occurred as prey at both study areas in 146–236 m on nine cruises during March, May, June, July, September, and October.

Wenner and Read (1982) reported *O. stephensoni* to be the second most common portunid collected in the South Atlantic Bight (10–227 m). It comprised 2% of all decapods caught between 111 and 183 m. Cain (1974) reported that *O. stephensoni* burrows by day and forages at night.

Other reef fish preying on *O. stephensoni* off North and South Carolina include warsaw grouper (*Epinephelus nigritus*) (Holbrook) (J. Dodrill, personal observation), red porgy (*Pagrus pagrus*), black sea bass (*Centropristis striata*) (Linnaeus), and vermilion snapper (juvenile crabs only) (South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982).

*Portunus floridanus* was represented by a single female (30.5 mm CW) swallowed intact by a grouper caught at 143–152 m during August 1985. Off North Carolina the species occurs from spring through fall on the outer shelf (50–100 m) but is not overabundant. Wenner and Read (1982) caught three specimens while trawling at 81 m at one of 496 stations between Cape Fear and Cape Canaveral. This species is associated with hard bottom and does not range north of our primary study area (Cain 1972, South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982).

*Calappidae*—*Calappa angusta* was the second most common decapod taken from snowy grouper caught in 108–201 m during 17 trips, all SSE of Cape Lookout. This crab occurred in every sampling month but May. *C. angusta* was represented by 34 males (21–40 mm CW), 5 females (22–34 mm CW), and 5 damaged specimens of undetermined sex. The predominance of male crabs and the presence of three of five recorded females in a single grouper stomach might indicate a spatial or temporal segregation by sex in depths of 146–155 m in the primary study area. Four *C. angusta* (30–34 mm CW) and nothing else in the intact stomach of a snowy

grouper caught 31 July 1985 in 146-155 m might also suggest a patchy distribution for this crab, or prey preference by the grouper.

The level of abundance indicated by occurrence in stomachs was not found by Wenner and Read (1982) from trawl sampling. They reported collecting only 45 specimens in 496 trawl tows in the South Atlantic Bight.

The presence of *C. angusta* in the stomachs of black sea bass and red porgy indicates some proximity to hard bottom areas (Manooch 1977, South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982).

*Acanthocarpus alexandri* ( $n = 13$ ) was the fourth most abundant decapod collected from snowy grouper stomachs. Specimens were adults or subadults represented by nine males (29-37 mm CW), three females (25-32 mm CW), and one damaged specimen, sex unknown. *A. alexandri* was found in stomachs in five trips in May, June, and August. Three specimens were taken from the same grouper caught in the primary study area at 146 m; all others were collected from grouper taken south of Cape Hatteras in 168-205 m. On a 5 May 1985 trip, two snowy grouper were caught in 196-205 m south of Cape Hatteras and both contained one *A. alexandri*. One grouper (925 mm TL) had four fresh, intact crabs in its stomach.

Wenner and Read (1982) collected only four *A. alexandri* at 496 trawling stations between 9 and 366 m in the South Atlantic Bight. *A. alexandri* was not collected by extensive dredging on the continental shelf off North Carolina (Cerame-Vivas and Gray 1966), although Pequegnat (1970) reported that this species was by far the most abundant deep water crab collected in the Gulf of Mexico.

*Leucosiidae*—*Myropsis quinquespinosa* ranked fifth in numerical prey abundance, with 10 individuals recovered. This decapod was found in snowy grouper caught in 146-159 m SSE of Cape Lookout on five trips during June, July, October, and November 1985. Three of these crabs were males (30, 33, 35 mm CW) and seven were females (24-41 mm CW). One 31-mm-CW female collected 15 July 1985 from a grouper caught in 155 m was ovigerous.

Wenner and Read (1982) collected this species in a narrow outer shelf depth range (102-155 m) with only 10 specimens trawled from 9 of 496 stations. Williams et al. (1968) reported 10 males and 1 ovigerous female (July) taken during four Duke University R/V *Eastward* cruises at eight stations in May, July, and October 1965 and in January 1966. Specimens were collected from the general vicinity of our fishing grounds on the shelf edge and upper slope between 100 and 210 m. Other central North Carolina outer



shelf collections of *M. quinquespinosus* in 120-160 m were reported by Cerame-Vivas and Gray (1966).

*Majidae*—*Stenocionops spinimana* was the sixth most abundant decapod prey, with nine specimens collected. Two male (34 and 36.5 mm CW) and seven female (34-56 mm CW) *Stenocionops spinimana* were taken from grouper caught south of Cape Lookout in 155-194 m. Collections were made on four trips in June, July, and September.

Wenner and Read (1982) reported only 18 isolated specimens from 496 trawl tows in the South Atlantic Bight in 60-170 m. Rathbun (1925) reported the species as deep as 227 m in the vicinity of our fishing area.

*Stenorynchus seticornis* was represented by one specimen obtained from a snowy grouper taken at 154 m in the primary study area in May 1985. The adult female (20 cm CW) had been swallowed intact and was still fresh when collected.

In contrast, this species was the second most abundant crab collected by Wenner and Read (1982) across a wide depth range (17-188 m) in the South Atlantic Bight. Off North Carolina the species has been collected at a variety of hard bottom and reef sites at inner-, mid-, and outer-shelf stations (to 100 m) (McCloskey 1968, Vernberg and Vernberg 1970, South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982).

In addition to being one of only two crab species reported from snowy grouper in the North Carolina BLM study (Duke University Marine Laboratory 1982), *S. seticornis* has been reported off North Carolina in the stomachs of at least two other reef fishes: white grunt (*Haemulon plumieri*) (Lacépède) and black sea bass (South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982). Randall (1967) also reported *S. seticornis* from three other epinpheline groupers: rock hind (*E. adscensionis*) (Osbeck), red hind (*E. guttatus*) (Linnaeus), and Nassau grouper (*E. striatus*) (Bloch). Visual studies of *S. seticornis* by Barr (1975) in the Virgin Islands indicated that the species is an opportunistic detritivore. It is most abundant on reef edges and is normally seen in greatest numbers at dusk and at night, when it moves to upper reef areas to feed.

*Nibilia antilocapra* was found once in a snowy grouper stomach taken in the primary study area from 137 to 146 m in August 1985. The individual (25 mm CW) was swallowed whole.

*Cancridae*—*Cancer irroratus* and *C. borealis* were the largest crustacean prey. *C. irroratus* was more prevalent in samples ( $n = 8$ ) than *C. borealis* ( $n = 2$ ). Both prey were taken only from large

(6.8-13.6 kg) grouper caught at depths of 194-236 m in June and July. They were represented by nongravid adults and were concurrent to the extent that one 900-mm grouper (TL) had eaten two *C. irroratus* (89 and 90 mm CW) and one *C. borealis* (83 mm CW) (total volume 197 mL).

Both species are common year-round in the decapod assemblage of the upper continental slope from the Chesapeake Bight south. *C. irroratus* and *C. borealis* ranked first and second among crabs trawled during fall and winter between Cape Hatteras and Cape Henlopen, Delaware (Musick and McEachran 1972). Wenner and Read (1982) ranked *C. irroratus* 15th, and *C. borealis* 18th numerically in 496 trawl stations in the South Atlantic Bight. At seven trawl stations between Charleston and Cape Lookout in 203-293 m, either *C. irroratus*, *C. borealis*, or both, were taken in six of seven tows (North Carolina Division of Marine fisheries, Cruise Reports, R/V *Dan Moore* cruise number 36, 26-28 September 1979). Cerame-Vivas and Gray (1966) reported rock crabs commonly occurring on the upper slope off North Carolina.

*Cancer irroratus* and *C. borealis* are found on several substrates. Jeffries (1966) reported separation by substrate in shallow waters off New England where *C. borealis* tended to associate with rocky habitat and *C. irroratus* with sand. Soto (1985) reported both species from mud bottom in the Florida Straits. Musick and McEachran (1972) noted both species trawled over sand, silt, clay, and coarse canyon sediments, though *C. borealis* seemed to be more stenothermal with a preference for rougher bottom.

*Parthenopidae*—*Parthenope pourtelesii* was represented by two intact females (22 and 36 mm CW) and one specimen of undetermined sex. They were taken from grouper caught on two trips (June, September) at 146 mm in the primary study area. This crab has been recorded over sand and sandy-mud bottoms (Powers 1977, Williams 1984).

*Solenoceridae*—*Solenocera atlantidis* (tentative identification) occurred in snowy grouper caught from May to September in the primary study area in 145-163 m. Seven of these shrimp were collected. Two species, *Solenocera atlantidis* and *Mesopenaeus tropicalis* Perez Farfante, numerically were among the top three decapod species trawled at depths of 56-183 m in the South Atlantic Bight (Wenner and Read 1982).

*Squillidae*—*Parasquilla coccea* was represented by a single individual taken from a grouper caught 6 August 1985 south of Beaufort Inlet, North Carolina in 148 m. It is a tropical stomatopod of the shelf edge and upper slope (82-382 m) and has not



been reported previously from North Carolina (R. Manning, Crustacean Section, National Museum of Natural History, Washington, D.C., personal communication).

#### PISCES

Fishes were the second most important major taxon in the diet, representing 6% of the food items and approximately 17% of the volume (Table 3). This is in contrast to Bielsa's (1982) analysis of 26 snowy grouper from the lower Florida Keys where fish comprised 43% of the prey items, 47% of the prey volume, and occurred in 69% of the intestines. The paucity of fish remains compared to crustacean remains was probably not a sampling artifact in our study, because selective regurgitation of fish, versus retention of hard-bodied crustaceans, was not evident from an examination of 23 intact stomachs (Table 4) nor from the NMFS and BLM data.

Fish in the snowy grouper diet were small (39-320 mm TL) and were swallowed whole. Thirty-three of 42 ingested fish were less than 200 mm TL. Small fish can be digested at a more rapid rate than adult brachyurans or large squid; thus, small fishes could be more important in the diet than our results show. In small fish, musculature rapidly separates, increasing the digestive surface area. Fish we recovered were either fairly fresh or in such an advanced state of digestion that they were unidentifiable. Only 15 of 42 fish could be identified to species, and of the 27 unidentifiable fish, most were under 200 mm TL.

Fish prey represent three general categories: small midwater schooling fishes often found near the bottom or in close association with rock relief, non-schooling reef fishes associated with irregular or hard bottom, and benthic fishes that burrow or remain concealed.

*Small, Schooling Fishes*—Seven butterfish (*Peprilus triacanthus*) (Peck) occurred as food during March and April in 146-225 m. A whole *P. triacanthus* (approximately 130 mm TL) was found in a snowy grouper on 20 April 1985 at a station south of Cape Hatteras in 194-225 m. A butterfish was also observed in a snowy grouper stomach from this area in late winter before our study (J. Dodrill, personal communication).

Butterfish can increase in abundance seasonally on the outer shelf and upper slope during cooler months off central North Carolina. This migratory trend is well documented from Cape Hatteras to southern New England, but is less apparent in more southern waters where the existence of a second, inshore population is hypothesized (S. Ross, North Carolina State University, personal communication; Murawski et al. 1977; Manooch 1984). The species tends

Table 4. Comparison of major food groups from snowy grouper overlapping with those of three other sympatric species of bottom fishes studied off North Carolina and South Carolina.

Prey Group	Predator			
	Snowy <sup>1</sup> Grouper	Vermilion <sup>3</sup> Snapper	Red <sup>2,4,5,6</sup> Porgy	Blueline <sup>7</sup> Tilefish
INVERTEBRATES				
Cephalopods				
(squid)	X	X	X	X
Stomatopoda	X	X	X	X
Calappidae	X	X (megalops only)	X	X
Cancridae	X			
Leucosiidae	X			
Majidae	X	X (zoea, megalops)	X	X
Parthenopidae	X	X	X	X
Portunidae	X	X	X	X
Scyllaridae	X	X	X	
Solenoceridae	X	X	X	X
FISH				
Caproidae	X			
Centriscidae	X			
Congridae	X		X	
Ophichthidae	X	X	X	
Serranidae	X	X	X	X
Stromateidae	X	X		X <sup>8</sup>
Synodontidae	X	X		X

<sup>1</sup> Present study central North Carolina specimens.

<sup>2</sup> Duke University Marine Laboratory (1982), North Carolina and South Carolina specimens.

<sup>3</sup> Grimes (1979), North Carolina and South Carolina specimens.

<sup>4</sup> South Carolina Wildlife Marine Resource Department (1982), South Carolina and Georgia specimens.

<sup>5</sup> South Carolina Wildlife Marine Resources Department and Duke University Marine Laboratory (1982), North Carolina specimens.

<sup>6</sup> Manooch (1977), North Carolina and South Carolina specimens.

<sup>7</sup> Ross (1982), North Carolina and South Carolina specimens.

<sup>8</sup> Personal Observation.



to remain close to the bottom by day, feeds on organisms on the bottom and in the water column, forms loose schools, and prefers sand instead of rock or mud bottom (Murawski et al. 1977).

We collected one juvenile red barbier (*Hemanthias vivanus* Jordan and Swain) (78 mm TL) from a snowy grouper caught 22 May 1985 in 146-155 m south of Cape Lookout. Parker and Ross (1986) reported large, fast-moving schools of juvenile *H. vivanus* (<150 mm TL) at 9 of 10 reef stations viewed from a submersible in 51-152 m off the central North Carolina coast.

Miller and Richards (1980) considered the red barbier an important reef indicator species in the South Atlantic Bight at depths greater than 55 m. The species has been observed hiding in reef crevices (R. S. Jones, Harbor Branch Foundation, Fort Pierce, Florida, personal communication). Therefore, schools periodically must be close enough to the bottom to be accessible to snowy grouper. The sister vessel fishing adjacent to the senior author's boat recovered several small (50-100 mm), reddish-orange serranids believed to be this species. At some deep reef areas (>180 m) such as the "Charleston Bump," 80 km east of Charleston, South Carolina, the yellow-fin bass (*Anthias nicholsi* Firth) displaces the red barbier as the most abundant small schooling serranid. Based on submersible observations during the summers of 1982 - 1983, R. S. Jones noted *A. nicholsi* was the most abundant reef fish. He hypothesized that anthiids could be an important grouper prey item, though stomachs yielded no food because of eversion (R. S. Jones, Cruise Reports, R/V *Johnson*, Cruise Number J-143 (III), 31 July-10 August 1982; Cruise Number J-158 (VI), 3-19 September 1983).

A vermilion snapper (305 mm TL) was found in the stomach of a snowy grouper (6.8 kg) taken in mid-November 1985 at 146 m, south of Cape Lookout. The vermilion snapper is one of the most common, commercially important schooling fish occurring over hard bottom on the mid and outer shelf off North Carolina. It is not surprising that small vermilion snapper in deeper water might fall prey to snowy grouper as they do in shallow water to speckled hind (*E. drummondhayi* Goode and Bean), gag (*Mycteroperca microlepis* Goode and Bean), and scamp (*M. phenax* Jordan and Swain) (South Carolina Wildlife Marine Resource Department 1982 South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982). Vermilion snapper were noted by the senior author as a snowy grouper prey item on at least one other trip made before our study.

*Nonschooling Reef Fishes*—A deepbody boarfish (*Antigonia capros* Lowe) (129 mm TL, intact) was taken from a snowy grouper caught

in May 1985 at 146 m. The boarfish is an outer shelf-upper slope species found over hard bottom with a tropical-subtropical distribution (Robins et al. 1986). *A. capros* is a common component of the ichthyofauna found in depths of 100-200 m from Cape Lookout southward (Wenner et al. 1979; North Carolina Division of Marine Fisheries, Cruise Reports, R/V *Dan Moore*, Cruise Number 19, Station Number 3332, 1-18 November 1977). Although trawl results and FAO species description profiles (Fischer 1978) suggest the species might be available to snowy grouper in small aggregations, deep reef submersible transects off Fort Pierce, Florida, and Charleston, South Carolina, reported this species either in pairs or singly, closely associated with rocky substrate (R. G. Gilmore, Harbor Branch Foundation, Fort Pierce, Florida, personal communication; R. S. Jones, Cruise Reports, R/V *Johnson*, Cruise Number J-43 (III) 31 July-10 August, Cruise Number J-158 (VI) 3-19 September 1983).

One longspine snipefish (*Macrorhamphosus scolopax*) (Linnaeus) (137 mm TL, intact), was collected on 29 April 1985 south of Cape Hatteras in the secondary study area in 201-238 m. Longspine snipefish are demersal inhabitants of the outer shelf-upper continental slope associated primarily with rocky substrate. They also reside over sand, where they have been taken in trawls (Fischer 1978). They are a temperate species with a probable worldwide distribution (Bigelow and Schroeder 1953, Hoese and Moore 1977, Fischer 1978, Robins et al. 1986). Submersible transects off Charleston, South Carolina on deep reefs in 180-220 m suggest that snipefish are available to grouper as scattered, non-schooling individuals that seek shelter in the reef or among attached hydroids (R. S. Jones, Cruise Reports, R/V *Johnson*, Cruise Number J-143 (III) 31 July-10 August 1982).

*Benthic Fishes*—Five ophichthis eels (165-272 mm TL) were recovered from snowy grouper stomachs; two were tentatively identified as *Myrophis punctatus* Lütken. Ophichthid eels are common prey of groupers and snappers (Robins et al. 1986). One ophichthid eel (252 mm TL), swallowed whole, was taken from a snowy grouper caught 29 June 1985 in 194 m SSE of Cape Lookout. The snake eel had penetrated tail first through the grouper's stomach, suggesting an augering motion during its death throes. The posterior half of the eel was encysted in the grouper's body cavity whereas the anterior portion in the stomach was being digested. Penetration by an ophichthid eel through a grouper's stomach has been reported by Breder and Nigrelli (1934), mentioned by Robins et al. (1986), and noted in sea bass (*Centropristis* sp.) by Link (1980) and Breder (1953).



Two cusk eels (Ophidiidae) occurred as prey in the primary study area. One specimen (110 mm TL) was from a 4.5-kg snowy grouper caught 17 May 1985 at 153 m, and a second (254 mm TL), tentatively identified as *Lepophidium jeannae* Fowler, was collected from a grouper caught 6 August 1985 in 192 m south of Cape Lookout. Typical of most snowy grouper fish prey, cusk eels are usually small ( $\leq 30$  mm TL) (Robins et al. 1986), benthic species which bury tail first into the sand (Böhlke and Chaplin 1968).

Two other benthic fishes, a congrid eel and an offshore lizardfish (*Synodus poeyi* Jordan) were removed from grouper stomachs. The former was a gravid female (320 mm TL) sampled 23 June 1985 from a grouper collected in 148 m south of Cape Lookout. The congrid (*Paraconger caudilimbatus*) (Poey) was reported from snowy grouper in the North Carolina BLM study (Duke University Marine Laboratory 1982). Large conger eels (*Conger oceanicus*) (Mitchell) ( $>1$  m TL), concealed or inactive by day but feeding at night in proximity to large *E. nivaetus*, are probably immune to snowy grouper predation.

The offshore lizardfish was a juvenile (86 mm TL) recovered 1 October 1985 in 148 m south of Cape Lookout. Offshore lizardfish were the sixth most numerically abundant fish species taken in Marine Resources Monitoring, Assessment, and Prediction Program bottom trawls in the South Atlantic Bight in the 111-183 depth range, comprising 2.2% of the fish caught at that depth (Wenner et al. 1979).

#### MOLLUSCA

Squid comprised almost 10% of the food volume (Table 3). Snowy grouper fed on at least two species, the long-finned squid (*Loligo pealei*) and the northern shortfin squid (*Illex illecebrosus*) (LeSueur). Squid occurred in grouper in June, July, September, and November.

*Loligo pealei* is a neritic species occurring over the continental shelf and upper slope to 400 m. It ranges throughout the water column at night and is demersal by day (Roper et al. 1984). Thus, *L. pealei* is available as food on or near the bottom in the daytime when snowy grouper are active feeders.

*Illex illecebrosus* was the second most common squid trawled at depths greater than 128 m, with numbers increasing beyond 219 m (North Carolina Division of Marine Fisheries, Cruise Reports, R/V *Dan Moore*, 1977-78). Wenner et al. (1979) reported that this species was more common on the upper slope (155-285 m). Shortfin squid might be a more important food for adult grouper toward the

deeper end of the grouper's bathymetric range. Two *I. illecebrosus* (130 and 175 mm mantle length) were swallowed intact by a 13.6-kg snowy grouper in 194 m in July 1985 south of Cape Lookout. Three *L. pealei* (142-, 130-, and 130-mm mantle length), two of which were taken from one 4.5-kg grouper, came from slightly shallower water, 146-155 m, in November. These specimens were swallowed whole. Although both species have been recorded from the same trawl tows, grouper appear to feed on unmixed groupings.

The few squid we found in stomachs might not indicate the value of this resource to snowy grouper. Probably only the gladius, eye lens, and beak are indigestible; digestion of other parts might proceed so rapidly that little remains. In winter, squid and fish might become more important in the diet. Seasonal abundance shifts might occur in some squids at that time, especially *L. pealei*, which is distributed over the shelf in spring and summer but concentrated on the outer shelf and upper slope in winter. Unfortunately, no extensive midwinter sampling was conducted to prove this; however, before the start of our study in early March 1985, grouper containing squid were caught beyond 183 m. Whole, frozen squid about the size found in grouper guts was the most effective bait.

The only other mollusk identified was a cone shell (*Concus delessertii*). The shell had a broken lip and worm tube inside, which suggests the grouper had picked up the shell empty.

#### FEEDING ECOLOGY

*Foraging Away From The Home Reef*—All snowy grouper aggregations we sampled were associated with hard bottom or wrecks. Sites were generally small, scattered, and surrounded by unproductive sand bottom. Grouper aggregations were similarly scattered and highly localized. Adult snowy grouper seem to associate exclusively with rugged bottom. This has been recorded in other studies off the southeastern United States (Low and Ulrich 1983; Parker and Ross 1986; R. S. Jones and R. G. Gilmore, Harbor Branch Foundation, Ft. Pierce, Florida, personal communication).

Limited exploratory fishing was undertaken to determine (1) if snowy grouper could be located over open, smooth bottom and (2) if this species foraged over open bottom any significant distance away from reef areas. Because solitary, large (>9 kg) mutton snapper (*Lutjanus analis*) (Cuvier) and red snapper (*L. campechanus*) (Poey), had been caught on experimental longlines set in less than 55 m over open bottom, we thought that snowy grouper might also be captured some distance from reefs. Twenty months of fathometer searching by two commercial vessels located no productive snowy grouper sites on open bottom between 128 and 247 m from south



of Cape Lookout to south of Cape Hatteras. Exploratory fishing was occasionally conducted over smooth bottom (247-305 m) where bait fishes were detected by the fathometer. No snowy grouper and only a few scorpionfish were caught. In addition to exploratory handline effort, a longline set was made over sand bottom south of Cape Lookout on 23 June 1985. Between 1245 and 1410 hours 102 hooks were fished in 240 m. No fish were caught, and most of the bait was untouched. Open bottom sets were discontinued for economic reasons.

We suspect that adult snowy grouper are sedentary, remaining at a specific reef site at least seasonally. During daylight hours they forage in the open, often near the top of the reef. They feed on small, schooling fish and squid, ambush slower moving decapods and non-schooling fishes, and occasionally move short distances onto sand or mud substrate adjacent to the reef to forage.

Direct observation to support territorial behavior of individual snowy grouper was impossible. Based on our experience with attempted release efforts of small (<335 mm) snowy grouper, an internally injured fish could not survive a 155-m descent to the bottom. However, three different observations lead us to hypothesize that groupers associate with a home reef on a seasonal basis. First, specific locations produced grouper for several consecutive months and in some cases over a period of at least 5 years. Second, on at least two occasions snowy grouper were caught with rusting circle hooks in their mouths. These hooks were the same type and size used on our previous trips to the sites when several uncrimped hooks were pulled from leaders. These fishing sites were virgin or were infrequently fished commercially. Third, a specific plastic teaser skirt was torn from the terminal tackle during one trip and recovered 6 weeks later in a 1.4-kg snowy grouper at the same 146-m site.

Snowy grouper probably move short distances from hard bottom to feed over sand or mud substrate. Single shelf-edge or upper-slope wrecks and specific reefs in 146-219 m have provided harvests of 22,680 kg or greater in a period of less than 3 months (L. Davidson, commercial fisherman, personal communication). Small areas are not likely to support such biomass even seasonally if the fish were restricted to feeding on or above hard bottom, unless feeding was restricted because of spawning or other activity.

A submersible observation of a large snowy grouper aggregation was made in late August 1979 slightly inshore of our fishing area (Parker and Ross 1986). Observers estimated nearly 8,000 snowy grouper per ha, 238 blueline tilefish per ha, and 79

speckled hind per ha in the vicinity of boulders at a depth of 125 to 137 m. Nearly all snowy grouper were over and immediately around the reef. However, some snowy grouper (24/ha), red porgy (660/ha), and silk snapper (*Lutjanus vivanus*) (Cuvier) (36/ha), were observed by day off to the side of the reef rooting in the sand, possibly for food (Parker and Ross 1986).

Longlines, which are not set directly on reefs, have been used extensively in the Carolinas, Georgia, Florida, and in the northern Gulf of Mexico since 1980. Snowy grouper represent part of the longline catch and thus might move short distances off the reef to take a bait. Also, an examination of decapod prey substrate preferences, as discussed previously, suggests that grouper might wander a short distance from hard bottom areas in search of food.

*Feeding Association with the Bottom*—Although our study indicates that snowy grouper feed both in the water column and on the bottom, grouper were always caught on or very near the substrate. Even in the case of large aggregations of grouper, fish were hooked no more than 3-4 m above the bottom. When currents lifted baits higher than this, no fish were caught. Identifiable markings of snowy grouper on the depth recorded were very close to the bottom. Examination of data from a trawl tow off southern North Carolina where 544 kg of adult snowy grouper were collected (North Carolina Division of Marine Fisheries, Cruise Reports, R/V *Dan Moore*, Cruise Number 20, 1969) revealed fish to be so close to the bottom that depth recorder markings of the fish were barely discernible.

Most snowy grouper foods are closely associated with the bottom. Even schooling fishes such as butterfish and red barbr, which can move up into midwater, as well as squids and portunid crabs, are commonly captured by bottom trawling.

*Feeding Mechanics*—Virtually every prey item had been swallowed whole. Except when limb autotomy had taken place in the stomach or through subsequent handling on deck, most decapods were intact. On two occasions prey were found alive in grouper throats: a deepbody boarfish and a crab (*Myropsis guinguespinosa*). Both were removed from grouper caught during daylight.

The intact condition of most prey in the stomachs supports the general feeding pattern of other grouper observed in the field (see Parrish 1987). The grouper either maneuvers close to the prey or waits in ambush, then opens its large mouth and expands its gill plates so abruptly that the prey is sucked whole into the mouth.

*Prey size, Grouper Speed, and Sedentary Behavior*—Prey size was surprisingly small for an adult fish as large as *E. niveatus*.



This might indicate a limit to the size of prey that a snowy grouper can chase down or consume whole. The largest crustacean prey, adult *Cancer* crabs, appeared to be restricted to large fish, those greater than 6.8 kg. However, this may be related to the tendency of larger grouper to inhabit the 146-228 m depths (Low and Ulrich 1983) where adult *Cancer spp.* are located.

Few fish more than 200 mm TL, and no fish more than 325 mm TL, were in the diet. This might result not only from an inability to swallow large prey whole, but also from an inability to pursue large fishes successfully. This stout-bodied, sedentary predator might not be able to capture these faster and more maneuverable species. Snowy grouper and tilefish both fed on blackbelly rosefish hooked on longlines off South Carolina, yet they were unable to catch this species when observed pursuing it (R. S. Jones, Harbor Branch Foundation, Cruise Reports, R/V *Johnson*, Cruise Number J-143 (III) 31 July–10 August 1982). Almaco jack (*Seriola rivirolana* Valenciennes), banded rudderfish (*S. zonata*) (Mitchell), and blueline tilefish were caught on handlines at the same time as snowy grouper, yet none was observed in stomachs.

Snowy grouper apparently are not fast swimmers, so it is not surprising that demersal decapods dominate their diet. Fast-moving fishes tend to be the target of quick, slender-bodied serranids such as the *Mycteroperca* groupers (Table 4). Speed is not a requirement for snowy grouper survival. One robust, 2-kg specimen without a caudal fin was caught. The blunted caudal peduncle was completely healed, and the fish appeared to be in good condition, although incapable of rapid propulsion.

Drift fishing suggests that snowy grouper are so sedentary that they will not pursue prey or move more than a few meters to intercept moving prey. Grouper locations on the reef sites were discrete, and the fish so sedentary that none was caught if the vessel missed the fathometer mark by a few meters. Sometimes fishermen standing only 7-m apart and using the same bait, gear, and fishing technique had drastically different levels of success. If only a portion of the vessel was over the mark, the nearest fisherman caught many fish, while others at end of the boat caught few. Grouper apparently would not pursue the bait once the lines had drifted off the reef.

*Day Versus Night Feeding*—More snowy grouper were caught in early morning or late afternoon than at midday or night. However, night capture of large snowy grouper and the presence of nocturnally active prey in their diet suggest that in addition to daylight feeding, large *E. niveatus* feed at night under certain condi-

tions. When large aggregations were present, fish were caught throughout the day. Only after fish were caught repeatedly during multiple drifts over a reef would catch rates decline, regardless of time of day.

Snowy grouper generally stopped taking baits at dusk. At depths beyond 183 m on calm, moonlit nights single large grouper (>9.1 kg) sometimes were caught. This contrasts with day catches when as many as eight small grouper (<4.5 kg) might take baits within a few seconds of each other.

The disparity in size of day versus night snowy grouper at the same station was noted in 194 m on 29 July 1985 SSE of Cape Lookout. A randomly measured sample ( $n = 44$ ) of specimens caught in daylight showed they were of mixed size (range = 465-950 mm, mean = 691 mm TL). That night, 37 large snowy grouper were caught at the same station between dark and 0400 hours. Fourteen representative specimens were measured revealing a narrower size range and larger average size (range = 890-990, mean = 921 mm TL) than those caught during the day.

*Competition*—Some other western Atlantic serranids, particularly members of the genera *Epinephelus*, *Hypoplectrus*, and *Serranus* have been found to prey heavily on crustaceans and less extensively on fishes (Parrish 1987). Conversely, *Mycteroperca* groupers feed almost exclusively on fishes (Table 4).

At depths beyond 137 m, adult snowy grouper compete to a limited degree with other grouper species, which are either uncommon or absent at these depths. Beyond 137 m only three other grouper species were recorded, all epinephelines: *E. mystacinus* (Poey), (*E. drummondhayi*), and *E. flavolimbatus* (Table 2).

Although the misty grouper (*E. mystacinus*) extends into our bathymetric fishing range and deeper in Bahamian, Caribbean, and Central American waters (Böhlke and Chaplin 1968; Robins et al. 1986; L. Davidson, personal communication), it is rare off North Carolina. Only two specimens (3-4 kg) were caught in 30 trips made in our study.

Speckled hind (*E. drummondhayi*) were as uncommon as misty grouper although they have been recorded at 130 m or less south of our fishing area, at times concurrently with small snowy grouper (Huntsman 1976, Manooch 1984). North Carolina and South Carolina headboats sampled by NMFS revealed only 18 speckled hind with food ( $n = 168$ ). Half contained fish (53% of all prey items; 65% of the volume). Decapods composed only 10% of all prey and 5% of the volume (Duke University Marine Laboratory 1982, Parrish 1987).



Yellowedge grouper (*E. flavolimbatus*) were sometimes caught with adult *E. niveatus* in deep water, but they represented only 1.0% of our total grouper catch (52 of 5,142 grouper in 30 trips). The species is uncommon in South Carolina commercial landings (Low and Ulrich 1983) and in commercial landings off southeast Florida (B. Hardy, Jupiter, Florida, personal communication). Diets of yellowedge grouper and snowy grouper probably overlap to some extent. The senior author noted that one yellowedge grouper had eaten a squid (17 May 1985 in 152 m) and another had swallowed whole a 65-75-mm, bicolored reef fish, probably a serranid. A third grouper collected 24 June 1985 from 148 m contained 18 *Portunus spinicarpus* (20-50 mm CW; 62.5 mL total volume). Parrish (1987) reported a squid in the stomach of a yellowedge grouper from the Virgin Islands. In the Gulf of Mexico where the yellowedge grouper is the dominant deep reef grouper, R. S. Jones (personal communication) saw them feeding on schooling anthiids and small reef fishes that were blinded by submersible lights.

Warsaw grouper (*E. nigrilus*) were extremely rare in our study. In 20 months of fishing, the only warsaw grouper caught (755 mm TL, 8.4 kg) was captured at 77 m southeast of Cape Lookout on 17 July 1985 (much shallower than *E. niveatus*). This grouper had consumed two crabs whole: *Calappa flammea* (90 mm CW; 105 mL total volume) and *Glyptoxanthus erosus* (Stimpson) (66 mm CW; 100 mL volume). Both crabs have bathymetric ranges normally not extending beyond 70-90 m (Williams 1984). *C. flammea* has been reported as snowy grouper prey, but probably from a fish taken in waters shallower than covered in our study (South Carolina Wildlife Marine Resource Department and Duke University Marine Laboratory 1982). In addition, the stomach from a 226-cm (190 kg) state record warsaw grouper was examined in September 1986. The stomach contained 13 *Ovalipes stephensoni* (70-80 mm CW). These crabs were swallowed whole and were in a similar state of digestion.

Food overlap of snowy grouper was compared with that of three other commercially important fishes that partially occupy the same bathymetric range as adult *E. niveatus* and for which food studies have been conducted (Table 5). Comparisons were based on 10 groups of invertebrates and 7 families of fishes. Red porgy contained 11 of the 17 categories, vermilion snapper contained 10 (excluding categories from which only zoea and megalopa were reported), and blueline tilefish contained 10 categories. Clearly, there is some dietary overlap, particularly with *E. niveatus* and *P. pagrus*, but competition on the upper slope is restricted by depth. Few red

Table 5. Percentage of contributions by volume of crustaceans and fishes to the diet of snowy grouper and other western Atlantic serranids.

Species	Source	Area	All Crustaceans	Crabs	Fish
<i>Epinephelus afer</i> Mutton hamlet	Randall (1967)	Caribbean	90.5	77.0	7.0
<i>E. fulvus</i> Coney	Randall (1967)	Caribbean	54.0	17.2	46.0
<i>E. adscensionis</i> Rock hind	Randall (1967)	Caribbean	75.1	66.7	20.1
<i>E. guttatus</i> Red Hind	Randall (1967)	Caribbean	69.9	39.5	21.1
<i>E. morio</i> Red grouper	Randall (1967)	Caribbean	81.1	12.2	13.3
<i>E. niveatus</i> Snowy grouper	This study	North Carolina	72.8	72.4	17.1
	See Parrish (1987)	North Carolina and South Carolina	72.0	72.0	28.0
<i>E. striatus</i> Nassau grouper	Randall (1967)	Caribbean	38.3	22.5	54.0
<i>E. cruentatus</i> Graysby	Randall (1967)	Caribbean	30.0	3.8	66.0
<i>Hyoplectrus aberrans</i> <sup>1</sup> Yellow-bellied hamlet	Randall (1967)	Caribbean	88.1	18.7	11.9
<i>H. chlorurus</i> <sup>1</sup> Yellowtail hamlet	Randall (1967)	Caribbean	75.0	17.1	25.0
<i>H. nigricans</i>	Randall (1967)	Caribbean	55.8	17.6	44.2
<i>H. puella</i> <sup>1</sup> Barrel hamlet	Randall (1967)	Caribbean	86.3	21.2	10.0
<i>Mycteroperca bonaci</i> Black grouper	Randall (1967)	Caribbean	0.0	0.0	100.0
<i>M. interstitialis</i> Yellowmouth grouper	Randall (1967)	Caribbean	0.0	0.0	100.0
<i>M. microlepis</i>	Naughton and Saloman (1985)	North Carolina	0.0	0.0	96.4
	Naughton and Saloman (1985)	South Florida	0.2	0.0	99.8
	Naughton and Saloman (1985)	West Central Florida	1.2	0.0	98.6



Table 5. Continued

Species	Source	Area	All Crustaceans	Crabs	Fish
	Naughton and Saloman (1985)	Northwest Florida	3.5	3.0	95.1
	See Parrish (1987)	South Carolina	0.2	0.0	96.0
<i>M. phenax</i> Scamp	Matheson et al. (1986)	North Carolina and South Carolina	1.0	0.5	90.0
	See Parrish (1987)	South Carolina	0.0	0.0	90.0
<i>M. spp</i> Scamp/yellowmouth	Nelson et al. (1986)	Texas Flower Garden	2.1	0.0	97.8
<i>M. tigris</i> Tiger grouper	Randall (1967)	Caribbean	0.0	0.0	100.0
<i>M. veneosa</i> Yellowfin grouper	Randall (1967)	Caribbean	0.8	0.0	95.3
<i>Paranthias furcifer</i> Creole-fish	Randall (1967)	Caribbean	79.2	0.0	0.0
	Nelson et al. (1986)	Texas Flower Garden	36.7	0.0	5.8
<i>Serranus tigrinus</i>	Randall (1967)	Caribbean	90.3	7.8	9.7
<i>S. tortugarum</i> Chalk bass	Randall (1967)	Caribbean	92.0	0.0	0.0

<sup>1</sup> All reported to be color phases of a single species, butter hamlet (*Hypoplectrus unicolor*).

porgy and vermilion snapper were caught beyond 142 m; none were caught in waters deeper than 165 m.

Grouping major foods into crustacean, fish, and squid categories revealed the following percentages of total food volume (mL): red porgy—49, 15, and 1% (Manooch 1977); vermilion snapper—38, 9, and 37% (Grimes 1979); blueline tilefish—64, 32, and insignificant percent, respectively (Ross 1982). Snowy grouper had values of 73, 17, and 10% for crustaceans, fishes, and squids, respectively (Table 3).

Snowy grouper feeding mechanics differ from those of blueline tilefish, vermilion snapper, and red porgy. Snowy grouper engulf prey whole by suction into their mouths. Red porgy and blueline tilefish might also employ suction but then use their strong teeth to

crush large prey as well as armored sessile organisms. Vermilion snapper feed on the bottom and to at least 5 m off the bottom, based on our fishing experience in 64-82 m. Most food items were pelagic, planktonic, or epibenthic (Grimes 1979) and were juveniles or larvae of many species (Dixon 1975, Grimes 1979).

*Prey Variability*—Snappers and groupers rely on many different types of foods; however, the diets of snappers are more diverse (Parrish 1987). The diet of adult snowy grouper included few prey species compared with other reef fishes caught at depths of 100 m or less. Prey categories, reduced to lowest taxa from our study combined with NMFS and BLM data, were 29 for snowy grouper, compared to 199 for vermilion snapper and 121 for red porgy (South Carolina Wildlife Marine Resource Department 1982). At depths of 100 m or less, hard-bottom faunal diversity is greater than at 140 m or deeper. Parrish (1987) suggested that where many species occupy small, discrete, hard-bottom areas, greater diet range reduced competition among reef fishes. Below a depth of 140 m many reef fish species disappear, and the need for a diversified diet to reduce feeding competition might be lessened for adult snowy grouper.

Intact grouper stomachs showed low prey diversity per individual stomach (Table 6). In a representative sample of 23 intact stomachs where no regurgitation appeared to have occurred, 16 stomachs had 1 species, 21 had 1 or 2 species, and only 2 had 3 or 4 species. A similar pattern was seen with the few *E. flavolimbatus* and *E. nigritus* stomachs examined (see Competition section).

There are three possible explanations for low species variability in an individual stomach. First, a large number of decapod species is not available in the limited depth range and geographic area sampled. Although Herbst et al. (1979) recorded 291 decapod species from Carolina shelf waters, Wenner and Read (1982) trawled only 54 species from the 111-183-m-depth range in the South Atlantic Bight, fewer than at inshore depth ranges of 28-55 m (87 species) or 56-110 m (84 species). Barans and Burrell (1976) reported 74 fish species trawled at 111-183 m in spring, declining to 43 species in summer. If we assume that snowy grouper are seasonally territorial and forage limited distances, prey possibilities for an individual fish during a specific feeding period are further reduced. Wenner and Read (1982), in 30-minute trawl tows at 111-183 m, averaged 3 decapod species and 25 individuals per tow.

Second, grouper are opportunistic feeders, focusing on whatever species are readily available, and they do not seek prey that is less common or more difficult to catch. For example, eight



Table 6. Summary of snowy grouper stomachs recovered intact with food captured off North Carolina, 1985.

Date	Size	Depth (m)	Food Item	Number	Volume (mL)
5/5/85	925 mm TL	196	<i>Acanthocarpus alexandri</i>	4	60
5/5/85	3.2 kg est.	205	<i>A. alexandri</i>	1	19
5/16/85	6.8 kg est.	154	<i>Portunus spinicarpus</i>	23	60
5/16/85	4.5 kg est.	154	<i>P. spinicarpus</i>	7	28
			fish vertebral column	1	1
5/22/85	3.2-4.5 kg	146	<i>P. spinicarpus</i>	15	30
5/22/85	3.6 kg est.	146-154	<i>P. spinicarpus</i>	7	22
6/2/85			<i>A. alexandri</i>	3	32.5
			squid frequent		6
6/10/85	13.6 kg est.	236	<i>Cancer irroratus</i>	1	150
6/21-24/85		148	<i>P. spinicarpus</i>	11	47
			small fish spines	2	1
6/21-24/85		148	<i>P. spinicarpus</i>	2	6.5
			<i>Calappa angusta</i>	1	9
			probable	1	5
			<i>Solenocera atlantidis</i>		
6/21-24/85		148	<i>P. spinicarpus</i>	12	34.5
6/21-24/85		148	<i>P. spinicarpus</i>	16	45
7/30/85	930 mm TL	194	<i>Ovalipes stephensoni</i>	1	98
			<i>Cancer irroratus</i>	1	150
			<i>Ilex illecebrosus</i>	2	220
			squid beaks	2	1
7/14/85	900 mm TL	194	<i>C. irroratus</i>	1	125
7/20-21/85	900 mm TL	194	<i>C. irroratus</i>	2	112
			<i>C. borealis</i>	1	85
7/31/85	2.3-3.2 kg est.	146-154	<i>Calappa angusta</i>	4	31
7/31/85	13.6 kg est.	194	<i>O. stephensoni</i>	1	50
9/4/85	9.1 kg est.	146-163	<i>O. stephensoni</i>	3	110
9/4/85	9.1 kg est.	146-163	<i>O. stephensoni</i>	1	50
9/6/85	9.1 kg est.	192	<i>Stenocionops spinimana</i>	2	59
9/20/85	850 mm TL	159	<i>O. stephensoni</i>	2	92
			<i>Myropsis quinquespinosa</i>	1	6
11/20/85	4.5 kg est.	146	<i>Rhomboplites aurorubens</i>	1	325
11/20/85	4.5 kg est.	150	<i>Loligo pealei</i>	2	175

intact stomachs contained 2-23 fresh *Portunus spinicarpus*, a total of 93 individuals. The only other remains found in these stomachs were two small, well-digested fish possible from previous feeding, one *Solenocera atlantidis*, and one bottom dwelling crab, *Calappa angusta*. Assuming that *P. spinicarpus* was locally abundant, snowy grouper apparently fed in the water column, ignored bottom organisms, and selected the most abundant prey at that site. At the same depth on the same day 2 km away, *P. spinicarpus* was not present in *E. niveatus* stomachs, nor were they on a later occasion at the original site. At other sites, feeding emphasis was on bottom-dwelling crabs, often adults of the same species and size or species with similar habits.

Third, low food variety within individuals might be volumetrically limited by the number of prey items that can be accommodated. Fewer large prey such as adult or subadult brachyurans will fit into the stomach of even a large snowy grouper. In one snowy grouper (930 mm TL), four food items, *Ovalipes stephensoni*, *Cancer irroratus*, and two *Ilex illecebrosus* totaled a volume of 486 mL, along with two additional squid beaks (1 mL). This was the greatest volume from any grouper stomach in our study (Table 5).

### CONCLUSIONS

The snowy grouper is one of the most important large, deep-reef, tertiary predators found on the outer continental shelf edge and upper slope off central North Carolina. An analysis of 5,088 snowy grouper, 335-1,100 mm TL, collected during 30 commercial bottom fishing trips in waters 137-238-m deep, revealed a diet dominated by crustaceans, particularly adult and subadult brachyurans (89.9% by number; 71.1% by volume). Small, benthic, midwater, schooling and nonschooling, reef-associated fishes (6.2% by number; 17.5% by volume) were of secondary importance, followed by squids (2.2% by number; 9.8% volume).

The abundance of decapods found in the diet might result from the reduced digestive rates for brachyurans compared to small (<200 mm TL) fish or squid. Crabs are also more accessible than fishes to slow-moving grouper, which probably feed by ambushing prey. In contrast to more slender, piscivorous *Mycteroperca* grouper species, snowy grouper probably are not capable of sustained or high-speed pursuit because of their stout bodies and sedentary nature. All prey were swallowed whole, and large brachyurans (*Cancer* sp., *Ovalipes stephensoni*) were found in larger grouper.

Slow speed, seasonal territoriality, apparent disuse of planktonic organisms or sessile invertebrates, absolute size of prey, and close association with the bottom probably limit variety of prey



taxa consumed as well as prey diversity in any feeding episode. After accounting for embolism, a low percentage of stomachs with food suggests irregular feeding.

Although there appears to be major food overlap with such congeners as *E. nigrinus* and *E. flavolimbatus*, these two species were uncommon in snowy grouper areas fished between 137 and 238 m. Prey item overlap was noted with three sympatric species, *Pagrus pagrus*, *Rhomboplites aurorubens*, and *Caulolatilus microps*, although competition for specific species was low (highest with *P. pagrus*). All three species seemed to have a more diverse diet than snowy grouper as well as different feeding strategies. *P. pagrus* and *R. aurorubens* were uncommon beyond 140 m and were absent beyond 165 m.

Snowy grouper are predominantly daylight feeders, and fishing success suggests greater feeding activity during morning or late afternoon. Small grouper generally feed only in daylight, whereas large individuals (>850 mm TL) at depths beyond 183 m, occasionally feed on calm, moonlit nights. Crepuscular or nocturnally active prey are sought at those times.

Snowy grouper are associated with the bottom and are confined almost exclusively to widely scattered, hard bottom, deep reef sites. Prey habits suggest grouper move short distances to feed. Extensive exploratory effort could not confirm the presence of grouper over open bottom areas away from hard bottom habitat of varying vertical relief.

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A Communal Winter Roost of Silver-haired Bats,  
*Lasionycteris noctivagans*  
(Chiroptera: Vespertilionidae)

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**ABSTRACT**—A communal roost of the silver-haired bat, *Lasionycteris noctivagans*, was found in January 1993 in Granville County, North Carolina. This is the first confirmed report of communal winter roosting for this species.

The silver-haired bat (*Lasionycteris noctivagans*) occurs in forested areas throughout much of North America (Kunz 1982) and is a common migrant and winter resident across North Carolina (Lee et al. 1982). This bat has been found in tree cavities and behind loose bark and, especially while hibernating in winter, will use a variety of shelters including buildings, mines, and rock crevices (Kunz 1982). It sometimes migrates in small groups (Barbour and Davis 1969), but is generally regarded as a solitary bat.

Most reports of large winter or summer aggregations were not considered reliable (Barbour and Davis 1969, Kunz 1982). Barbour and Davis (1969) attributed to C. H. Merriam (1884a and 1884b) two reports that suggested *L. noctivagans* occasionally forms nursery colonies; however, Merriam did not make either observation. One report of 13 young bats found in a crow's nest near Lowville in Lewis County, New York, was told to Merriam by Frank Hough some years after the discovery. Merriam (1884b:92) included this report under the *L. noctivagans* account stating that they "presumably were of the species now under consideration, because it is by far the most common in the region." Additionally, Merriam (1884b:93-94) printed an anecdotal report of a summer aggregation described to him in a letter by William Brewster. While looking for woodpeckers on 18 June 1880 along the shores of Lake Umbagog, New York, Brewster found a colony of bats in a snag. He reported that there were "certainly hundreds and probably thousands" of bats, and he described them all as adults of the same "small dark-colored" species, "which as you [Merriam] suggest, was probably *Vesperugo* [*Lasionycteris*] *noctivagans*." No specimens were saved, and Merriam's decision to include this report under the *L. noctivagans* account appears based on the vague physical description and Merriam's as-

section that this was the most common bat in the area. There is one summer record of a family of silver-haired bats found in an abandoned woodpecker hole (Novakowski 1956).

Several sightings of pairs of *L. noctivagans* roosting together in winter have been reported. Notes by N. B. McCulloch, in the files at the N.C. State Museum of Natural Sciences, describe a male and female *L. noctivagans* found together in a house in Raleigh, North Carolina (Wake County), on 11 December 1951. Brimley (1897) wrote that two were taken 26 December 1892 from a hollow tree in Bertie County, North Carolina, but did not note the sex of either. Barbour and Davis (1969) also reported finding two *L. noctivagans*, hibernating about 3 feet from each other, in a mine in Illinois. No information was provided on the sex of these. While conducting field investigations of rabies in wildlife, Pearson (1962) visited silica mines to sample bats and recorded occasions when more than one *L. noctivagans* was found, but he did not describe the roost associations.

Several sources described multiple *L. noctivagans* found in a single locality, but it is unclear whether any of them were found roosting together. Frum (1953) took six *L. noctivagans* from the same sandstone ledge in West Virginia on two different dates in March, but no comments on roost associations were made. Brimley (1897) reported taking four on 9 July 1891 in Bertie County, North Carolina, but there were no comments on whether the bats were taken from a roost or whether they were shot while flying.

On 10 January 1993 I received two silver-haired bats that had been obtained by Matt Shimmel (Raleigh, North Carolina) while he was looking for old lumber for carpentry projects in Granville County, North Carolina. He found the bats behind cardboard that had been nailed as insulation to the inside of wooden walls of an abandoned house. The bats fell to the floor when the cardboard was lifted, and his efforts to get them to hang back on the wall failed. Fearing the bats would die if left there, Shimmel retrieved them and contacted me. He told me there had been several more bats behind the cardboard, perhaps as many as eight.

I kept the two bats in a refrigerator (at a temperature ranging from 4 to 5 C), until 25 January 1993, when I visited the house in Granville County (about 2.4 km northeast of Grissom) to return them to the capture site. At that time I found three other *L. noctivagans* behind the piece of cardboard where I was told the other two had been found. They were roosting 1.75-2.0 m above the floor of the



house. Before they were exposed, the bats vocalized when the cardboard was lifted, but otherwise they were lethargic and moved slowly. They roosted close to each other, but were not touching.

The temperature behind the cardboard where the bats were roosting was 6 C at 1615 EST. One of the three bats found on 25 January weighed 10.6 g (a female), the other two (one male and one female) each weighed 11.1 g. The two I received from Shimmel on 10 January were both females. Their masses on 26 January were 10.6 and 10.0 g. Nearby (approximately 0.75 km) another abandoned, dilapidated house also had cardboard nailed to the walls. I checked behind the cardboard and found a single male *L. noctivagans*, weighing 10.6 g. Both houses were open and offered little protection from the elements. In fact, the room in the second site where I found the *L. noctivagans* had only two intact walls. Both houses were located at the edges of mature, second-growth oak forest. The communal winter roost that I observed appears to be the first confirmed report of more than two *L. noctivagans* using the same roost.

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# A Preliminary Body Fat Index for Cottontails (Lagomorpha: Leporidae)

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**ABSTRACT**—Total body fat is frequently used as an indicator of an animal's physical condition, but its determination requires post-mortem analysis. A field index of total body fat useful on live cottontails (*Sylvilagus floridanus*) was developed. I collected a small sample of cottontails in April 1984 to determine total body fat. Carcasses were homogenized and assayed for ether extraction of crude fat. A significant regression equation predicting the natural log of crude fat expressed as a percentage of dry mass from the natural log of the mass/head-length was developed.

An animal's plane of physical condition is considered directly related to the abundance and quality of life's necessities in the habitat, which ultimately affect population productivity (Martin 1977). Body fat reserves are commonly used to indicate an animal's physical condition, which in turn, can be used to infer habitat quality or rate of population increase (Caughley 1970, Martin 1977). I had particular interest in determining the feasibility of developing a quick field index of body condition for use in mark-recapture, radio telemetry, and other investigations of live eastern cottontails.

In previous studies, Havera (1977) found that total percentage of carcass fat was the best indicator of the condition of fox squirrels (*Sciurus niger*), and Robel et al. (1974) found that total carcass fat was related to food quality in northern bobwhite (*Colinus virginianus*).

Indices of fat content are often practical surrogates for the much more costly laboratory determinations of total body fat. Finger et al. (1981) used a kidney fat index, which proved to be correlated with total body fat of white-tailed deer (*Odocoileus virginianus*). Bamford (1970) found significant correlation between both abdominal and kidney fat indices and total body fat. Riney (1955) developed a kidney fat index, and combined fat measures have been used by Anderson et al. (1969, 1972). Martin (1977) used an abdominal fat index for indicating fat reserves in European wild rabbits (*Oryctolagus cuniculus*). Bamford (1970) found a significant relationship between a length:standardized-mass ratio and total body fat in the brush-tailed possum (*Trichosurus vulpecula*). Bailey (1968) reported on the use of mass/length (nose tip to tip of fur on fully extended hind feet) as an index of physical condition in

cottontails, but did not present substantiating data on total fat or other physical condition.

The objectives of my study were (1) to identify a postulated relationship between a morphometric measure of body size and total body fat in cottontails and (2) to develop a field index for body condition of live cottontails. I present preliminary evidence that a mass:length ratio was significantly correlated with total body fat in a small sample of cottontails in North Carolina. I also discuss development of a field index using mass/head-length as a predictor of the percentage of total body fat, an indicator of body condition.

### METHODS

During April 1984 12 cottontails were trapped or shot from three different study sites in the North Carolina Piedmont. Total length (nose tip to tail tip) was measured with a tape; head length (nose tip to back of skull at posterior edge of lambdoidal crest) was measured with calipers. Animals were weighed with a spring scale and were frozen within 4 hours for later laboratory analysis. When collected, two of the heaviest animals, collared as part of an earlier telemetry study, had skin lesions caused by the collars, and had dropped in rank to second and third lowest in terms of crude fat. These values were retained in the analysis.

Frozen cottontails were weighted with a Mettler digital balance. I used frozen masses obtained on the digital balance in preference to fresh masses obtained with a spring balance because of the greater precision of the former and later determination that the spring scale might have been unreliable. Specimens were homogenized before assay of crude fat. In preparation for homogenizing, hair was shaved to avoid clogging the homogenizer, carcasses were sliced laterally, and digestive tracts were cleaned. Animals were autoclaved for 30 minutes to soften tissues and masticated with a laboratory homogenizer (Janke & Kunkel IKA Werk Ultra-Turrax Type T45-S4). Homogenate from each animal (500-600 mL) was dried for 4 days in a ventilated oven and was stirred twice daily to break up crust and to promote drying. Triplicate 2-g samples were weighed and oven-dried for 5 hours for percentage of dry-mass determination. Triplicate 2-g samples were weighted into extraction crucibles for determination of ether extract (Pickel extraction of crude fat) expressed as a percentage of oven-dried tissue mass.

Because of the small sample size I investigated relationships between body measurements and total fat with single dependent variable models for both sexes combined. A natural log transformation normalized the distribution of fat content as shown by normal probability plots and the Shapiro-Wilk W-test (SAS Institute, Inc. 1990)



( $P < 0.05$ ). Examination of residuals revealed apparently randomly distributed error.

### RESULTS

Total masses ranged from 1,022 to 1,364 g and averaged 1,176 g (SE = 33). Total lengths ranged from 29.2 to 45.7 cm and averaged 33.9 cm (SE = 1.7). Head length ranged from 7.20 to 9.70 cm and averaged 8.49 cm (SE = 0.20). Crude fat ranged from 3.7 to 12.6% and averaged 7.2% (SE = 0.8) of tissue dry mass. Coefficients of variation of fat content among triplicate samples from each animal were all less than 5%. Females generally had higher (but not significantly higher) fat content than did males.

Crude fat content was significantly correlated to total mass ( $P = 0.04$ ) and to head length ( $P = 0.09$ ), but not to total length measurements ( $P = 0.9$ ). The best predictive equation (Fig. 1) was

$$\log_e(\% \text{ crude fat}) = 2.78957 \times \log_e \left( \frac{\text{Mass(gm)}}{\text{Head Length(cm)}} \right) - 11.85897$$

This equation was highly significant ( $P = 0.007$ ) and had an  $r^2$  of 0.697.

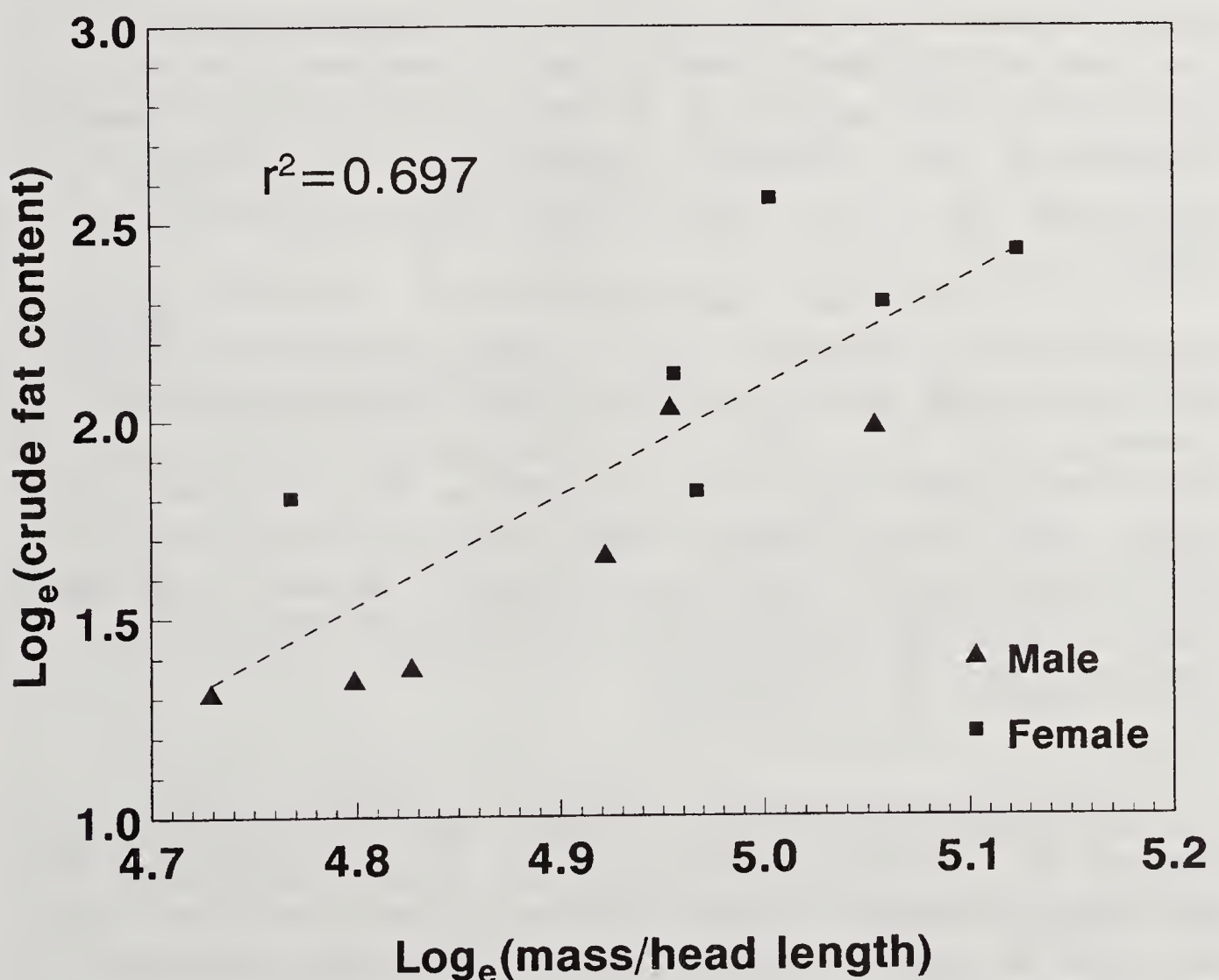


Fig. 1. Regression of crude fat content and mass/head-length of collected cottontails.

## DISCUSSION

My sample, though admittedly small, nonetheless produced a strongly significant relationship between a mass:length ratio (head length, in this case) and total body fat content in cottontails in the area studied. Total mass and head-length, in particular, are readily obtained from live cottontails handled by one person in the field. Because of the demonstrated relationship between the index and total body fat content, the index could indicate habitat quality for cottontails, though the relationship between body fat and habitat could be complex.

Jacobson et al. (1978) postulated a positive correlation between adequacy of diet and fat stores. Chapman et al. (1977) observed a geographic gradient of increasing body fat in western Maryland coinciding with increasing severity of winter weather. Thomas (1987) however, postulated that leporids could optimize fat storage with the likelihood of predation and starvation so that rabbits in low quality habitats would tend to begin winter with higher fat levels than those in better quality habitats. Jacobson et al. (1978) and Chapman et al. (1977) observed seasonal fluctuations in several condition and fat indexes as well as variations between sexes, though female cottontails tended to be in better condition in the spring than were males. Due to possible sex and season effects on body fat, sex ratios of samples and the season of application should be standardized. This preliminary model should be verified on an independent set of data before being used as a predictor of fat content.

Lack of significant relationship between fat and body length could have been partly due to inaccurate measurements caused by inconsistent body extension. Bailey (1968) described such error in measuring total body length (tip of nose to tip of fir at end of fully extended hind legs) of live cottontails. Use of calipered head-length avoids errors related to body extension. If sufficiently accurate measurements of total length could be obtained, total length might prove to be a better predictor. Usefulness of other body dimensions should be investigated.

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Diets of Marsh Rabbits,  
*Sylvilagus palustris* (Lagomorpha: Leporidae),  
from Coastal Islands in Southeastern North Carolina

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**ABSTRACT**—Dietary analyses were conducted for marsh rabbits from barrier and dredge-material islands near Wilmington, North Carolina. Marsh rabbits primarily consumed upland vegetation, especially during the summer and winter, and they ate a wide variety of plant species available to them. Forbs and grasses comprised the bulk of the diet; shrub utilization was low, even in winter.

Diets of marsh rabbits, *Sylvilagus palustris* (Bachman), are poorly known despite the local abundance of these herbivores in wetland habitats in the southeastern United States. Blair (1936) conducted feeding trials in Florida using captive marsh rabbits to check for acceptance of particular wetland plants, and his results have been cited by others describing the diet of marsh rabbits (Chapman and Willner 1981, Chapman and Feldhamer 1982). Diets of free-ranging marsh rabbits, however, have not been described in any part of the range of the species. The purpose of this investigation, therefore, was to determine the diets of marsh rabbits inhabiting estuarine islands in southeastern North Carolina.

#### METHODS

Islands in southeastern North Carolina are of two types: low, narrow barrier islands separated from the mainland by marshes and the Atlantic Intracoastal Waterway, and small oval-shaped islands adjacent to the Waterway where the U.S. Army Corps of Engineers deposits dredged material. Because vegetative zonation and species composition on these islands are similar (Parnell and Soots 1979, Hosier and Eaton 1980) and marsh rabbits are common to abundant on both island types, we combined data from both island types to increase sample sizes.

Floristic diversity and abundance (from Braun-Blanquet approximations for 0.25-m<sup>2</sup> plots at 3-m intervals along four to six transects across each island) were used to describe the plant communities from which rabbits were taken. Six communities were defined: low marsh, high marsh, grass flat, shrub thicket, dune, and berm. Reference slides for 78 species of plants taken along these transects were prepared for use in comparisons with plant fragments

Table 1. Abundance (percentage of diet attributable to plant), followed by range (in parentheses), of flora consumed by marsh rabbits on estuarine islands in southeastern North Carolina. Asterisks indicate significant seasonal variation in consumption.

Plant species	Abundance			
	Spring (n = 5)	Summer (n = 9)	Winter (n = 7)	Total (n = 21)
<i>Low Marsh</i>				
Spike grass ( <i>Distichlis spicata</i> )*	9 (19)			3 (19)
Seablite ( <i>Suaeda linearis</i> )	1 (7)	5 (42)		2 (42)
Seabeach orach ( <i>Atriplex arenaria</i> )	<1 (2)			<1 (2)
Sea lavender ( <i>Limonium carolinianum</i> )	6 (18)			2 (18)
<i>High Marsh</i>				
Reed ( <i>Phragmites australis</i> )* <sup>a</sup>	12 (59)			4 (59)
Marsh sedge ( <i>Fimbristylis spadicea</i> )		<1 (1)	<1 (1)	<1 (1)
Black needlerush ( <i>Juncus roemerianus</i> )		1 (13)		<1 (13)
Marsh pink ( <i>Sabatia stellaris</i> )	3 (8)		<1 (1)	1 (8)
Silverling ( <i>Baccharis halimifolia</i> )	<1 (1)			<1 (1)
Sea ox-eye ( <i>Borrchia frutescens</i> )	1 (6)			<1 (6)
<i>Grass Flat</i>				
Wild rye grass ( <i>Elymus virginicus</i> )	<1 (6)			<1 (6)
Muhly ( <i>Muhlenbergia capillaris</i> )		<1 (3)		<1 (3)
Finger grass ( <i>Chloris petraea</i> )		4 (4)		1 (4)
Saltmeadow cordgrass ( <i>Spartina patens</i> )	13 (44)	4 (15)	17 (42)	11 (45)
Foxtail grass ( <i>Setaria geniculata</i> )	4 (19)	7 (52)		4 (52)
Bunch grass ( <i>Panicum virgatum</i> )		3 (18)		1 (18)
Sedges ( <i>Cyperus</i> spp.)	2 (7)	2 (12)	<1 (3)	1 (12)
Dayflower ( <i>Commelina erecta</i> )	1 (5)	2 (9)		1 (9)
Cottonweed ( <i>Iresine rhizomatosa</i> )	2 (5)	11 (31)		4 (31)
Marsh pennywort ( <i>Hydrocotyle bonariensis</i> )	7 (36)	2 (15)	11 (39)	7 (39)
Morning glory ( <i>Ipomoea sagittata</i> )		4 (16)	3 (18)	2 (18)
Blue curl ( <i>Trichostema</i> sp.)			<1 (2)	<1 (2)
Buttonweed ( <i>Diodia teres</i> )	5 (24)			2 (24)
Bedstraw ( <i>Galium</i> spp.) <sup>b</sup>	8 (38)		6 (29)	5 (38)
Seaside goldenrod ( <i>Solidago sempervirens</i> )	9 (14)	12 (45)	10 (20)	10 (45)
Camphorweed ( <i>Heterotheca subaxillaris</i> )*		8 (49)	35 (30)	14 (51)
Firewheel ( <i>Gaillardia pulchella</i> )	6 (28)	<1 (2)		2 (28)
<i>Shrub Thicket</i>				
Greenbriar ( <i>Smilax</i> spp.) <sup>c</sup>	<1 (2)			<1 (2)
Beach pea ( <i>Strophostyles helvola</i> )*	<1 (1)	25 (64)		8 (64)
Yaupon ( <i>Ilex vomitoria</i> )	7 (33)		9 (18)	5 (33)
Vir. creeper ( <i>Parthenocissus quinquefolia</i> )		1 (11)		<1 (11)
Creeping cucumber ( <i>Melothria pendula</i> )		1 (8)		<1 (8)



Table 1. Continued.

Plant species	Abundance			
	Spring (n = 5)	Summer (n = 9)	Winter (n = 7)	Total (n = 21)
<i>Dune</i>				
Purple sandgrass ( <i>Triplasis purpurea</i> )	<1 (1)	<1 (4)	1 (7)	1 (7)
Sea oats ( <i>Uniola paniculata</i> )		2 (14)		1 (14)
Lovegrass ( <i>Eragrostis pilosa</i> )			2 (13)	1 (13)
Sandspur ( <i>Cenchrus tribuloides</i> )		5 (15)	<1 (1)	2 (15)
Panic grass ( <i>Panicum amarum</i> )		<1 (4)	1 (9)	<1 (9)
<i>Berm</i>				
Dune elder ( <i>Iva imbricata</i> )			<1 (1)	<1 (1)
Unidentified forbs	3 (10)	<1 (1)	4 (7)	2 (10)
Unidentified grasses	<1 (1)	<1 (3)	<1 (2)	<1 (3)

<sup>a</sup> *Phragmites australis* (= *P. communis*)  
<sup>b</sup> includes *Galium tinctorium* and *G. hispidulum*  
<sup>c</sup> includes *Smilax bona-nox* and *S. laurifolia*

recovered from rabbit stomachs. The methods of fixing and staining plant epidermal tissues and microtechniques for diet analysis were modifications of those used by Dusi (1949).

Rabbit collections were made during three periods coinciding with new plant growth in the spring (March 1987), abundant green forage of late summer (August/September 1986), and sparse old growth in winter (December 1986). Relative ages of rabbits were determined by the degree of fusion between the exoccipital-supraoccipital suture (Hoffmeister and Zimmerman 1967). Stomachs were fixed in 10% formalin and stored in 45% isopropanol.

Stomach contents were removed and gently agitated in 45% isopropanol to mix the fragments. A random sample was drawn from the slurry and was stained in a 10-mg/L Rhodamine B solution for 48–72 hours. Twenty subsamples were drawn from each sample and were mounted on clean slides. Five fields of view were selected, using a chart of random coordinates, for each of the 20 slides. Fragments were identified by diagnostic epidermal characteristics and comparison with reference slides. Unidentifiable fragments were recorded as either unknown grass or forb. For each plant species, dietary data are expressed as abundance, or proportion of the diet attributable to that plant.

Principal component analysis indicated that the abundance of plants found in marsh rabbit stomachs varied seasonally but without regard to age and sex; therefore, rabbits of all ages and both sexes

were combined for the analysis of seasonal variation. Chi-square was used to test the hypothesis that marsh rabbits display no significant ( $P < 0.05$ ) seasonality in plant consumption using transformed (square root) abundance data.

## RESULTS

*Spring*—The spring collection included five marsh rabbits. There were 25 species of plants identified from the stomachs of these rabbits, with each stomach averaging eight species (range = 6-10). Diets of individual rabbits were varied, and no plant appeared to be dominant during this period (Table 1). Grasses accounted for 41% of the spring diet, whereas forbs comprised 52% and shrubs 7%. Marsh vegetation comprised 32% of the diet, and together with plants typical of the adjacent low grasslands, accounted for 89% of the diet. Spike grass (*Distichlis spicata*), sea lavender (*Limonium carolinianum*), and reed (*Phragmites australis*) collectively comprised 27% of the spring diet; these marsh plants were not eaten in summer and winter (Table 1).

*Summer*—Nine marsh rabbits were collected during August and September. Twenty-five plant species were found in their stomachs, although each stomach averaged eight species (range = 5-11). Beach pea (*Strophostyles helvola*) was the dominant plant in the stomachs of most rabbits collected during summer and accounted for 25% of the total diet (Table 1). Beach pea, seaside goldenrod (*Solidago sempervirens*), and cottonweed (*Iresine rhizomatosa*) accounted for 48% of the cumulative diet of these rabbits. Forbs averaged 70% of the diet with grasses contributing 29% and shrubs 1%. Marsh vegetation comprised 6% of the diet for this season.

*Winter*—The winter diet was examined in seven marsh rabbits. Seventeen plant species were represented, with each stomach containing an average of seven species (range = 5-10). The abundance of camphorweed (*Heterotheca subaxillaris*) was higher in winter than in other seasons, representing 35% of the diet (Table 1). Camphorweed and saltmeadow cordgrass (*Spartina patens*) were consumed by all rabbits collected in winter and together averaged 52% of the diet. Forbs (including camphorweed) accounted for 70% of the diet, whereas grasses and shrubs comprised 22% and 8%, respectively. Marsh vegetation accounted for less than 1% of the diet.

*Combined*—We found 40 species of plants in the stomachs of 21 marsh rabbits collected in spring, summer, and winter (Table 1). Five species were eaten year-round, especially marsh pennywort (*Hydrocotyle bonariensis*), seaside goldenrod, and saltmeadow cordgrass, with seasonal shifts in the importance of each. Marsh vegetation was relatively more important in spring, with significant consumption of



spike grass ( $\chi^2 = 6.00$ , 2df,  $P < 0.05$ ) and reed ( $\chi^2 = 6.91$ , 2df,  $P < 0.05$ ). Marsh rabbits primarily consumed upland vegetation during summer and winter, with significantly higher consumption of beach pea ( $\chi^2 = 10.00$ , 2df,  $P < 0.01$ ) in summer and camphorweed ( $\chi^2 = 6.01$ , 2df,  $P < 0.05$ ) in winter than in other seasons. Rabbits consumed nearly equal amounts of grasses and forbs in spring, but their dependence on forbs increased to more than double the consumption of grasses during summer and winter. Shrubs did not contribute a major portion of the diets, even in winter. Thirty-eight other species of plants were found along the transects but were not consumed by the marsh rabbits we collected (Appendix A).

## DISCUSSION

Tomkins (1935) noted that marsh rabbits in coastal Georgia fed in dunes and upland areas adjacent to wet marshes on dredge-material islands, but he did not identify the plants upon which these rabbits were feeding. Our study, despite relatively small sample sizes, indicates that marsh rabbits forage extensively in upland communities on estuarine islands in southeastern North Carolina, and that they eat a wide variety of plant species available to them. Blair (1936) offered captive marsh rabbits plants common to Florida swamp habitats where he collected the rabbits. Some plant species (or related species) eaten by Blair's rabbits were also found in the island communities of our study and were eaten in southeastern North Carolina as well. These plants included greenbriars (*Smilax*), pennyworts (*Hydrocotyle*), hollies (*Ilex*), silverling (*Baccharis*), and rushes (*Juncus*). Blair (1936) noted that marsh pennywort was relished by captive rabbits. In our study, consumption of marsh pennywort averaged 7% in spring, 2% in summer, and 11% in winter.

In southeastern North Carolina marsh rabbits rely on saltmeadow cordgrass, pennywort, and seaside goldenrod throughout the year; other species of plants are consumed seasonally, especially beach pea in summer and camphorweed in winter. MacCracken and Hansen (1984) noted that Nuttall's cottontails (*S. nuttalli*) also tended to utilize many of the same species year-round with seasonal shifts in the importance of species. Holloran et al. (1981) found that eastern cottontails (*S. floridanus*) in Virginia consumed more forbs in summer and fall than in winter and spring, with grasses forming the bulk of the diet in winter and spring. Other cottontail species have been shown to display seasonal shifts in reliance on forbs, grasses, and shrubs mostly in response to availability and environmental conditions (Dalke and Sime 1941, Turkowski 1975, Green and Flinders

1980, MacCracken and Hansen 1984). The consumption of different species at different times of year may be related to the water content (Getz 1966, Dunson and Lazell 1982), availability of nutrients and secondary compounds (de la Cruz and Poe 1975), or the amount of fiber in different stages of plant growth cycles.

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Appendix A. Species of plants found on estuarine islands in southeastern North Carolina but not found in stomachs of marsh rabbits.

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*Low Marsh*

- Smooth cordgrass (*Spartina alterniflora*)
- Glasswort (*Salicornia virginica* and *S. europaea*)

*High Marsh*

- Cattail (*Typha* sp.)
- Wax myrtle (*Myrica cerifera*)
- Seashore mallow (*Kosteletskyia virginica*)
- Marsh elder (*Iva frutescens*)
- Marsh aster (*Aster tenuifolius*)

*Grass Flat*

- Foxtail grass (*Setaria magna*)
- Broomsedge (*Andropogon virginicus* and *A. scoparius*)
- Yucca (*Yucca aloifolia* and *Y. filamentosa*)
- Mexican tea (*Chenopodium ambrosioides*)
- Prickly-pear (*Opuntia drummondii* and *O. compressa*)
- Climbing milkweed (*Cynanchum palustre*)
- Ragweed (*Ambrosia artemisiifolia*)
- Dog-fennel (*Eupatorium capillifolium*)
- Climbing hempweed (*Mikania scandens*)

*Shrub Thicket*

- Red cedar (*Juniperus virginiana*)
- Live oak (*Quercus virginiana*)
- Pokeweed (*Phytolacca americana*)
- Red bay (*Persea borbonia*)
- Blackberry (*Rubus* spp.)
- Black cherry (*Prunus serotina*)
- Hercules'-club (*Zanthoxylum clava-herculis*)
- Muscadine grape (*Vitis rotundifolia*)
- Wild lettuce (*Lactuca canadensis*)

Appendix A. Continued.

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*Dune*

American beach grass (*Ammophila breviligulata*)  
Croton (*Croton punctatus*)  
Seabeach evening-primrose (*Oenothera humifusa*)  
Ground-cherry (*Physalis maritima*)  
Horseweed (*Erigeron canadensis*)

*Berm*

Russian thistle (*Salsola kali*)  
Seabeach amaranth (*Amaranthus pumilus*)  
Sea rocket (*Cakile harperi*)  
Seaside spurge (*Euphorbia polygonifolia*)



Notes on the Geographical and Ecological Distribution of  
Relict Populations of *Synaptomys cooperi*  
(Rodentia: Arvicolidae) from Eastern North Carolina

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**ABSTRACT**—As part of a study to evaluate the effects of forest management on North Carolina pocosin communities, small mammals were trapped between May 1991 and May 1992 in 15 stands in Carteret, Craven and Jones counties, North Carolina. Captures included three *Synaptomys cooperi*, extending the known range of the species in eastern North Carolina about 170 km south of Dismal Swamp localities. These specimens, and others collected since 1977, indicate that the paucity of records between 1896 and the 1970s is the result of ineffective trapping methods and insufficient fieldwork in appropriate habitat. *S. cooperi* is more widely distributed in eastern North Carolina than previously reported. Populations are disjunct and appear to be Pleistocene relicts.

The southern bog lemming, *Synaptomys cooperi*, occurs in eastern North America (Fig. 1) from southeastern Canada west to western Minnesota, and south to southwestern Kansas, northeastern Arkansas, southeastern Tennessee, and western North Carolina (Linzey 1983.). A population in the Dismal Swamp in Virginia and North Carolina is disjunct and is recognized as a separate subspecies, *S. c. helaletes* (Wetzel 1955). For almost a century this subspecies was known only from 24 specimens collected between 1895 and 1898 (Handley 1979). Between 1977 and 1980, field work in the Dismal Swamp (Rose 1981) and in adjacent areas in northeastern North Carolina yielded additional specimens of *S. c. helaletes*, some from new localities, but all in close proximity to the Dismal Swamp (Rose 1981, Lee et al. 1982). This subspecies is now con-

sidered to be common in many habitats in that area (Rose et al. 1990, Handley 1991).

Before 1989 *S. cooperi* had been reported in eastern North Carolina only from Gates, Pasquotank, and Perquimans counties (Brimley 1905, Rose 1981, Lee et al. 1982). After intensive trapping on the Dare Country mainland, often in what might be regarded as optimal habitat for the species, Clark et al. (1985) concluded that *S. cooperi* did not occur south of the Albemarle-Pamlico peninsula. Four specimens collected between 1989 and 1992 proved that conclusion erroneous. An *S. cooperi* was captured in Beaufort County in 1989 (Webster et al. 1992), and in 1991 and 1992 M.S.M. and K.S.K. captured three *S. cooperi* in Jones and Craven counties in the Croatan National Forest. The National Forest captures were about 170 km south of the southernmost Dismal Swamp record and approximately 57 km south of the Beaufort County record.

To better understand populations of *S. cooperi* in the Dismal Swamp and eastern North Carolina (Fig. 1), we describe the circumstances of the National Forest captures, review the ecology of these populations in southeastern Virginia and eastern North Carolina, and discuss the disjunct distribution of this species in the region.

## METHODS

*Study site description*—Small mammals were trapped in and around the Croatan National Forest in parts of Carteret, Jones and Craven counties (Fig. 1). The 382,716-ha National Forest is generally bounded by the Neuse River to the north, the Trent and White Oak rivers to the west, White Oak River and Bogue Sound to the south, and the Atlantic Ocean to the east. There are five spring-fed shallow lakes totaling 10,617 ha in the National Forest. The wide variety of habitat types there includes timberlands, sand ridges, long-leaf pine (*Pinus palustris*) savannah, blackgum-cypress (*Nyssa sylvatica*-*Taxodium* spp.) swamp, Carolina bays, and some of the largest pocosins in the state.

Pocosins are distinct freshwater wetlands formed on deep peat deposits. Dominant pocosin vegetation includes evergreen shrubs (*Cyrilla racemiflora*, *Ilex coriacea*, *I. glabra*, *Lyonia lucida*), dwarf pond pine (*Pinus serotina*), and bay trees (*Gordonia lasianthus*, *Magnolia virginiana*, *Persea borbonia*). Pocosins can vary considerably in species composition, tree density, and stature of the vegetation (Ash et al. 1983). Pocosins where all of the vegetation is stunted and the community is dominated by shrubs are called





Fig. 1. The locations of records of *S. cooperi* from eastern Virginia and North Carolina are indicated by dots. Dots in Virginia represent specimens from the Dismal Swamp. Counties in North Carolina discussed in the text are identified by numbers: 1. Beaufort, 2. Craven, 3. Dare, 4. Gates, 5. Jones, 6. Pasquotank, and 7. Perquimans. The blackened area on the map of North America shows the current range of *Synaptomys cooperi*.

short pocosins. Tall pocosins are characterized by a taller understory and are generally dominated by pond pines.

To establish baseline data on pocosin mammals and to describe the changes in these communities associated with intensive forest management, M.S.M. and K.S.K. selected 15 stands in natural and managed pocosin communities for small mammal sampling. Three stands each represented five treatments: three managed habitats—open canopy, closed canopy, and thinned—and two natural stands—short pocosin and tall pocosin. The nine managed stands were in pine plantations on the periphery of the Croatan National Forest (on Weyerhaeuser Company land), and the six natural pocosin areas were within the Croatan National Forest.

One short pocosin stand was in the interior of the Great Lake Pocosin, and one tall pocosin stand was on its periphery. The highest elevations in the National Forest are in the Great Lake Pocosin, which has no history of anthropogenic modification and is one of the largest contiguous expanses of short pocosin in the state.

*Small mammal trapping*—Trapping was conducted for three field seasons: summer 1991, winter 1992, and summer 1992. Snap traps and pitfall traps were used each field season. Snap traps were active for 5 consecutive nights; pitfall traps were active 7. One-hundred snap traps (Museum Specials and Victor rat traps), baited with a mixture of peanut butter, rolled oats, and raisins, were set in each stand. There were five trap-lines per stand. In the first two field seasons pitfall traps were located at the end of each trap-line. Pitfalls with drift fences were added in the interior of each stand in the last field season (see Mitchell 1992 for details).

*Vegetation sampling*—Vegetation data were collected to provide a context for interpreting faunal community structure. Parameters for overstory, shrub layer, herbaceous vegetation, and fallen dead material were evaluated for each stand (see Mitchell 1992 and Karriker 1993 for details).

*Specimen identification*—Specimens collected were deposited in the North Carolina State Museum of Natural Sciences (NCSM) where they were identified and were placed in the research collection as vouchers. Skull measurements used by Wetzel (1955) to separate subspecies of *S. cooperi* were compared to measurements taken from the skulls of two specimens (NCSM 6778 and NCSM 7190) collected in the National Forest. The skull of the other specimen (NCSM 7191) was that of a juvenile and was not compared because Wetzel analyzed only adults.



## RESULTS

*Small mammal trapping*—We recorded 22,206 snaptrap-nights and 3,322 pitfall trap-nights. The projected trap quota was not achieved primarily due to a wildfire which burned one short pocosin stand while traps were in place. A total of 926 small mammals, representing 15 species, were trapped, and at least ten other mammals or their sign were recorded from the study area (Table 1) (Mitchell 1992).

Table 1. Number of mammals collected or observed in the Croatan National Forest, 1991 and 1992.

Species	Open canopy	Closed canopy	Thinned	Pocosin		Total trapped
				Short	Tall	
<i>Didelphis virginianus</i>	*1	*	2	0	0	2
<i>Sorex longirostris</i>	8	19	16	46	19	108
<i>Blarina brevicauda</i>	14	18	15	19	5	71
<i>Cryptotis parva</i>	14	0	0	0	0	14
<i>Scalopus aquaticus</i>	0	*	0	0	0	0
<i>Sylvilagus floridanus</i>	*	*	0	*	0	0
<i>Sylvilagus palustris</i>	*	0	1	*	*	1
<i>Sciurus carolinensis</i>	0	0	*	0	0	0
<i>Oryzomys palustris</i>	10	2	1	0	0	13
<i>Reithrodontomys humulis</i>	69	2	29	21	0	121
<i>Peromyscus leucopus</i>	4	0	12	20	1	37
<i>Peromyscus gossypinus</i>	0	15	17	0	48	80
<i>Ochrotomys nuttalli</i>	20	34	27	40	79	200
<i>Sigmodon hispidus</i>	186	2	55	0	0	243
<i>Microtus pinetorum</i>	0	0	0	12	0	12
<i>Mus musculus</i>	20	0	0	0	0	20
<i>Synaptomys cooperi</i>	0	0	0	2	1	3
<i>Procyon lotor</i>	*	*	*	*	*	0
<i>Ursus americanus</i>	*	*	*	*	*	0
<i>Lynx rufus</i>	*	*	*	0	*	0
<i>Canis</i> spp.	*	0	*	*	*	0
<i>Urocyon cinereoargenteus</i>	0	0	0	0	*	0
<i>Lutra canadensis</i>	*	*	*	0	0	0
<i>Mustela frenata</i>	0	0	0	1	0	1
<i>Odocoileus virginianus</i>	*	*	*	*	*	0
Totals	346	92	175	161	153	926

<sup>1</sup> An asterisk (\*) denotes a sighting or sign observed.

Table 2. Percent cover and dominant species in the canopy, midstory, and understory of sampled treatments, Croatan National Forest, 1991 and 1992.

Treatment	Canopy		Shrub		Herbaceous	
	% cover	Species	% cover	Species	% cover	Species
Managed stands						
Open canopy	11	<i>Pinus taeda</i>	56	<i>Lyonia lucida</i> <i>P. taeda</i>	79	<i>Adropogon</i> spp. <i>Arundinaria gigantea</i>
Closed canopy	98	<i>P. taeda</i>	58	<i>Ilex</i> spp. <i>L. lucida</i>	16	<i>Osmunda cinnamomea</i> <i>Smilax</i> spp.
Thinned	91	<i>P. taeda</i>	59	<i>Ilex</i> spp. <i>L. lucida</i>	24	<i>Eupatorium capillofolium</i> <i>Rubus</i> spp.
Natural						
Short pocosin	4	<i>P. serotina</i>	97	<i>L. lucida</i> <i>Zenobia pulverulenta</i>	16	<i>O. cinnamomea</i> <i>Smilax</i> spp.
Tall pocosin	97	<i>P. serotina</i> <i>P. taeda</i>	67	<i>L. lucida</i> <i>Cyrilla racemiflora</i>	4	<i>A. gigantea</i> <i>Smilax</i> spp.



Capture success varied considerably between field seasons with rates of 2.5, 2.1, and 6.5% recorded for each respective season. Species composition within the treatments was relatively consistent among the field seasons.

Three *S. cooperi* were trapped in 2 of the 15 stands. Two were taken in snap traps, one in a pitfall trap. All captures of *Synaptomys* were from natural pocosin stands associated with the Great Lake Pocosin. Two were taken in the short pocosin stand, and one was taken from the periphery at the tall pocosin stand.

*Vegetation sampling*—The percent cover and dominant species in the canopy, midstory, and understory of all sampled treatments is presented in Table 2. The short pocosin stand where two *S. cooperi* were taken was dominated by shrubs that rarely exceeded 1 m in height. It had an open canopy primarily composed of pond pine (*Pinus serotina*) with a few loblolly bay trees (*Gordonia lasianthus*). Trees were sparsely distributed, stunted, and poorly developed. Dominant shrubs were fetterbush (*Lyonia lucida*), titi (*Cyrilla racemiflora*), red bay (*Persea borbonia*), loblolly bay, young pond pine, zenobia (*Zenobia pulverulenta*), and sweetbell (*Leucothoe* spp.). Dominant herbaceous species included cinnamon fern (*Osmunda cinnamomea*), pitcher plant (*Sarracenia* spp.), and sphagnum moss (*Sphagnum* spp.)

The average height of the overstory in the tall pocosin stand where one *S. cooperi* was captured was 13 m. Dominant trees were pond pine and loblolly bay; the shrub layer height averaged 1.5-3 m. The most common shrubs were fetterbush, loblolly bay, small gallberry (*Ilex glabra*), titi, and huckleberry (*Gaylussacia* sp.). There was little herbaceous vegetation, only sparsely distributed *Smilax*.

*Specimen identification*—Based on geographic proximity, the specimens are expected to represent *S. c. helaletes*, a race previously regarded as endemic to the Dismal Swamp region. The subspecific identity of the National Forest specimens is not clear from the skull measurements. We compared these measurements to those of the *S. c. stonei* and *S. c. helaletes* specimens that were measured by Wetzel (1955) (Table 3). Wetzel's conservative treatment of the adult category precludes subspecific determination by skull measurements because none of the National Forest specimens had all characteristics used by Wetzel to place them in the adult category.

## DISCUSSION

The habits of the southern bog lemming certainly contribute to the low capture rates for this rodent. A. K. Fisher found *Synaptomys*

Table 3. Summary of selected cranial measurements from 10 adult *Synaptomys cooperi helaletes* and 26 adult *S. c. stonei* from the Southern Appalachians (Wetzel 1955) compared to measurements of two specimens (NCSM 6778, NCSM 7190) taken in the Croatan National Forest, 1991 and 1992.

Measurements	<i>S. c. stonei</i>		<i>S. c. helaletes</i>		NCSM 6778	NCSM 7190
	$\bar{x}$	SD	$\bar{x}$	SD		
Width of upper incisors	3.5	0.01	4.0	0.03	3.9	3.8
Condylbasilar length	24.8	0.08	25.1	0.20	25.2	24.7
Nasal width	3.4	0.04	3.5	0.07	3.2	3.6
Zygomatic width	16.7	0.11	17.1	0.22	16.4	16.4
Height of skull	10.1	0.08	10.5	0.17	9.3	9.2

“hard to catch, because it will not take any sort of bait; the only way to capture it is to set a trap in its runway” (cited in Handley 1979:325). Rose et al. (1990) described *S. c. helaletes* as an enigmatic study subject, noting that sign was observed 10 months before they caught 11 *S. c. helaletes* in only a few weeks. There is some evidence that pitfall traps and live traps might be more effective than snap traps for capturing *S. c. helaletes* (Rose et al. 1981, Rose et al. 1990). We could not compare trapping methods for *S. cooperi* in the National Forest because only three individuals were caught.

Insufficient field effort in appropriate habitat might also account for low capture rates. Previous studies (Handley 1979, Breidling et al. 1983) in the Great Dismal Swamp only sampled forested sites. Rose (1981) trapped both forested and nonforested sites in the Dismal Swamp, and all of his *S. c. helaletes* captures were from nonforested areas. Rose’s study sites varied from purely herbaceous vegetation to natural or planted pine stands up to 15 years old. Some were taken from a grassy remnant marsh, others were captured under an electrical powerline where the 40-m-wide right-of-way was dominated by giant cane (*Arundinaria gigantea*) and softstem rush (*Juncus effusus*). Rose (1981) stated that as long as grasses remained in the understory, *S. c. helaletes* persisted.

A review of the habitat descriptions from other captures demonstrates that *S. c. helaletes* can be found in a variety of successional communities. The data tag for a specimen (AMNH 265071) captured in Gatesville, Gates County, reads “young-2-3' pine plantation on cleared forest land.” The Pasquotank County specimen (NCSM 4019) obtained from a barn owl pellet certainly came from



open habitat. The Beaufort County specimen was captured in a pit-fall trap set in the ecotone between communities characterized as a xeric pine savannah and a lowland pocosin (Webster et al. 1992). There is no detailed habitat information available for the Perquimans County record (Brimley 1905) or for two other specimens (NCSM 2654 and NCSM 4019) taken in the Dismal Swamp area. Although trapping in the Croatan National Forest yielded specimens from only unmanaged stands, it is clear from other efforts that some human alterations create habitats suitable for this lemming.

There are few structural differences between the three short pocosin stands sampled in the National Forest that could account for the presence of *Synaptomys* in one and not in the other two. Drainage in the Great Lake Pocosin is limited to ditches associated with roads on the pocosin's boundary, remote from its interior. By contrast, the other two stands of short pocosin where no *Synaptomys* were caught were considerably smaller and were bounded on at least two sides by ditches. The Great Lake Pocosin interior has a greater degree of surface saturation than the other areas, as evidenced by the abundance of *Sphagnum* observed in the interior.

The lack of records of *S. c. helaletes* from 1897 to the 1980s was once believed to be the result of changes in habitats caused by human activities (Handley 1979), particularly those involving changes in the water table. Rose (1981) concluded that fire prevention probably had a greater negative effect on *Synaptomys* habitat than did draining and ditching because the exclusion of fire reduced the number and size of natural openings. Succession in pocosin communities is naturally suppressed; therefore, pocosins provide a diverse assemblage of early successional habitats. These habitats are one of the few natural, open canopy plant communities in the southeastern Coastal Plain. Lee (1986) considered that pocosins might have provided the only available local habitat for many early successional birds before colonial development. Pocosins appear to play a similar role for *S. cooperi* in eastern North Carolina.

Because *S. cooperi* has now been captured both to the north and south of the Albemarle-Pamlico peninsula, one would assume that *Synaptomys* can be found in appropriate habitat on the peninsula as well. Dare County has large expanses of pocosin and other wetlands, and it is separated from the Dismal Swamp area only by Albemarle Sound. No *Synaptomys* were taken in the 1980s on the Dare County mainland even though it was intensively trapped by both Clark et al. (1985) and by U.S. Fish and Wildlife Service personnel at the Alligator River National Wildlife Refuge (Mike

Phillips, Refuge Manager, personal communication). Trapping frequency has been high and efforts have covered all wetland and upland habitats, so it is unlikely that *S. cooperi* occurs on the Albemarle-Pamlico peninsula.

Doutt et al. (1973) suggested that the major feature common to all *Synaptomys* habitats was that they were marginal for *Microtus*, and Linzey (1983) documented competitive exclusion of *Synaptomys* by *Microtus* in Virginia. Results from the National Forest investigation and Clark et al. (1985) seem to lend further support to this relationship. No *Microtus pinetorum* were caught in the National Forest stands in which *Synaptomys* were captured, but 13 *M. pinetorum* were caught in one of the other short pocosin stands. Additionally, *M. pennsylvanicus* was abundant in wet, early successional communities on the Dare County mainland (Clark et al. 1985).

The geographic distribution and genetic structure of modern populations are determined by historical patterns of dispersal as well as current ecological associations. The presence of *S. cooperi* south of the Dismal Swamp is not unexpected when one considers that the late Pleistocene range of *S. cooperi* extended much farther southward than the present range. Pleistocene fossil records are known from as far south as Citrus County, Florida (Linzey 1983). In Wetzel's (1955) examination of the subspeciation and dispersal of the southern bog lemming, he determined that *S. c. helaletes* does not differ so greatly from the nearest form (*S. c. stonei*) as did the other subspecies he studied. The close relationship was attributed to a relatively recent loss of interconnecting range.

Pocosin habitats might have provided refugia for species at the extreme limits of their distributions since the Pleistocene. Thermal properties of evergreen vegetation and saturated soils characteristic of pocosins likely provide a buffer from temperature extremes. Clark et al. (1985) reviewed the role of late Pleistocene climates as they relate to some small mammal distributions in the southeastern United States and noted that in pocosin areas both northern and southern faunal elements co-exist in local refugia supported by subclimax communities.

Zoogeographically, a number of Atlantic Coastal Plain mammals presently reach either northern, southern, or eastern limits of distribution in pocosin-rich areas. Other taxa formerly believed to be confined largely to the Dismal Swamp, such as *Blarina brevicauda telmalestes* and *Microtus pennsylvanicus nigrans*, have been documented south of the Dismal Swamp area (Lee et al. 1982, Clark et al. 1985). The star-nosed mole (*Condylura cristata parva*) also has a broader distribution on the southeastern Coastal Plain



than previously believed (Paradiso 1959, Lee 1987), and records reported here demonstrate a similar distributional pattern for *Synaptomys cooperi*.

Although we were unable to make a subspecific determination from the National Forest sample of *S. cooperi*, further taxonomic investigation is warranted. Eight of the 13 cranial measurements used by Wetzel to distinguish the *S. cooperi* subspecies did not show significant differences between *stonei* and *helaletes*. The unclear subspecific identity of the specimens reported here could be a result of a wider and more southern distribution of *S. c. stonei* in the past. Individuals captured in southeastern North Carolina might be a relict population of that race, or represent an intergrade between *S. c. stonei* and *helaletes*.

### CONCLUSIONS

In general, the new records of *S. cooperi*, along with the recent captures of other small mammals in eastern North Carolina that were once thought to have narrower distributions, emphasize the need for more small mammal investigations in wetlands and associated habitats. Considering the wide variety of early successional habitats that *S. cooperi* has been captured in, and the abundance of those habitats in eastern North Carolina, it seems reasonable to expect that *S. cooperi* is widespread there. Based on the National Forest trapping results and other studies, it appears that populations in this region are disjunct.

More specimens of *S. cooperi* are needed to better understand the taxonomy of these disjunct populations. Future surveys for *S. cooperi* should include trap methods other than snap-trapping and should encompass a variety of both natural and managed early successional communities.

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Responses of Deer Mice, *Peromyscus maniculatus*  
(Mammalia: Rodentia), to Wild Hog Rooting in the  
Great Smoky Mountains National Park

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**ABSTRACT**—A mark-recapture study was conducted to assess the impacts of wild hog (*Sus scrofa*) rooting on small mammal populations in the upper elevation beech (*Fagus grandifolia*) forests of the Great Smoky Mountains National Park. Small mammals were captured using live traps and pitfalls. Microhabitat variables were measured in the vicinity of each live trap site and analyzed using discriminant function analysis. Populations of cloudland deer mice (*Peromyscus maniculatus nubiterrae*) showed no significant differences between rooted and unrooted sites and are apparently unaffected by rooting. Although the presence of other small mammals was noted on both rooted and unrooted sites, deer mice were the only mammals caught with sufficient frequency to allow statistical analysis. Discriminant analysis of microhabitat variables indicates that deer mice orient toward areas dominated by deciduous trees with heavy midstory cover and light ground cover. We hypothesize that habitat selection by deer mice in this ecosystem is dominated primarily by predator avoidance.

A population of exotic European wild hogs entered the boundaries of Great Smoky Mountains National Park sometime during the

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1940s or 1950s (National Park Service Uplands Field Research Laboratory, 1985, European wild hogs in Great Smoky Mountains National Park). Since that time their population has spread throughout the Park, damaging its rich flora and fauna (Bratton 1975, Singer 1981). The upper elevation beech forests have received especially heavy impact because of their small total acreage, rich herbaceous layer, and preferential rooting by hogs in summer (Bratton 1974, Singer et al. 1981). Research has been conducted on the effects of rooting on the flora of these areas, but very little work has addressed the effects of rooting on the animal communities (Bratton 1974, Howe et al. 1981, Lacki and Lancia 1983, Singer et al. 1984).

The objective of our study was to evaluate the responses of deer mice and other small mammal populations to wild hog rooting in the beech forest in the following ways: (1) compare populations of deer mice and other small mammals on rooted and unrooted sites, (2) identify important microhabitat variables for trap success and failure, and (3) determine if the presence or absence of important microhabitat variables affects population levels at each site.

## METHODS

### SITE SELECTION

Russell (1953) and Whittaker (1956) defined the Gray Beech Forest or "beech gaps" in the Great Smoky Mountains National Park. These gaps are beech (*Fagus grandifolia*) forests that occur between 1,430 and 1,800 m in elevation (Bratton 1975) and are usually found on south-facing slopes on the ridge that bisects the Park in a northeast-southwest direction (Russell 1953). These gaps occur as small islands of deciduous trees in spruce-fir (*Picea rubens*-*Abies fraseri*) forests.

We grouped our beech gap study sites into rooted or unrooted categories based on history and intensity of hog rooting. Selection of unrooted (or control) sites and rooted sites was made difficult by the high variability of hog densities, the widespread and uniform distribution of the hogs within the Park, and the ephemeral nature of some small mammal populations. Because it is impossible to say that any beech gaps exist that have never been rooted, we use the term "unrooted" to refer to sites that appeared undisturbed at the time of our study. We selected three rooted and three unrooted trap sites each year. Sites were comparable in elevation, slope, and aspect.

### MAMMALS

*Sampling*—We livetrapped small mammals for five trap-nights on each site with Sherman live traps arranged in a 6 x 6 grid with



10-m spacing. Trapping was conducted from 3 July through 11 August in 1989 and 28 June through 4 August in 1990. We baited traps with sunflower seeds packaged in a bag of cheesecloth and suspended in the back of the cage. Baiting traps with a mixture of rolled oats and peanut butter in the beginning of 1989 attracted foraging bears (*Ursus americanus*) to the trap sites. These bears destroyed a significant number of traps at each site, effectively shutting down the trap grid. Each captured small mammal was identified to species, sexed, aged (juvenile or adult), weighed, toe clipped for future identification, and released.

In 1990, we added pit-fall traps because of the lack of shrew captures during the 1989 field season. Pits were constructed by burying a 1-gallon plastic planter along a fallen log, lining the planter with plastic, and filling it about one-third full with water. Ten pit-fall traps were interspersed among each live trap site, with one or two pit-fall traps per live trap line. All animals collected from pit-falls were identified according to species, weighed, and when possible, aged and sexed.

*Data Analysis*—We used Program CAPTURE (Otis et. al. 1978, White et. al. 1982) to analyze data from the Sherman live traps for the capture of deer mice. CAPTURE selected the appropriate population model for the data and calculated a population estimate and capture probabilities for each site. Because of insufficient capture rates, no data on small mammal species other than deer mice from the live traps and no data from the pit-fall traps were analyzed with CAPTURE. We combined the results of the 1989 and 1990 CAPTURE analyses and tested them with a two-way ANOVA (alpha level = 0.05) to determine if (1) pooling the data would reveal significant differences between rooted and unrooted sites, (2) there were differences in overall populations between the two years, and (3) there were any significant interaction effects between year and rooting class.

#### VEGETATION

*Sampling*—We selected 20 variable classes for measurement at each trap. Table 1 contains a list of the variable classes measured and the method by which measurements were taken. Several of the classes (e.g., percent species cover) involved measurements for each plant species represented. Therefore, the number of variables considered is greater than the number of variable classes. The point-quarter method for sampling trees followed that suggested by Phillips (1959). We defined overstory as woody vegetation >7.5-cm dbh and

Table 1. Microhabitat variable classes selected for measurement.

Stratum	Variable Class	Method
Overstory	canopy closure	densiometer
	nearest tree size	point-quarter
	nearest tree distance	point-quarter
Understory	nearest tree size	point-quarter
	nearest tree distance	point-quarter
Over/understory	richness	species total
	% evergreenness	point-quarter
Shrub	% total cover	line intercept
	% species cover	line intercept
	richness	species total
Herb	% total cover	line intercept
	% species cover	line intercept
	richness	species total
Forest floor	log diameter	dbh tape
	log distance	tape measure
	% bare soil	line intercept
	% exposed rock	line intercept
	% leaf litter	line intercept
	depth leaf litter	ruler
Soil	resistance	penetrometer



the understory as woody vegetation  $>2$  m in height and  $<7.5$ -cm dbh. Snags and odd limbs (living or dead) touching the ground were included in these measurements because deer mice are known to preferentially use snags for refuges (Wolff and Hurlbutt 1982), and only small woody trunks are required for escape routes. The shrub layer was defined as all vegetation between 0.4 and 2.0 m in height and the herb layer as all vascular vegetation in the 0.0-0.4-m range. Our use of the line intercept method followed Hays et al. (1981) and consisted of laying out two 2.5-m transects in random directions from the center of each trap.

During the 1990 field season several variables were not measured: measurements involving the shrub layer, percentages of individual herb species cover (except for greater star chickweed, *Stellaria pubera*, and spring beauty, *Claytonia virginica*), herb richness, percent bare soil, percent leaf litter cover, and soil resistance were omitted because analysis of the 1989 data indicated these variables were not significant. We chose not to use the dbh of the closest overstory and understory tree in 1989, but included it in the 1990 analysis. Barry et al. (1984) found that deer mice oriented towards larger trees.

*Data Analysis*—We performed a series of discriminant function analyses on microhabitat data to determine the most important variables. To “identify” truly important microhabitat variables, we believed it was important to test the ability of variables to classify the success or failure of a trap to capture a small mammal and to produce a directional relationship consistent with known animal ecology (Tacha et al. 1982).

To begin the discriminant analysis, we pooled the data from the measured variables for all six sites each year. Variables were grouped as belonging to successful or unsuccessful live traps. We defined a successful trap as any live trap with one or more captures and an unsuccessful trap as having no verified captures. All variables represented as percentages were arcsine transformed before analysis to approximate normal distributions. We performed a correlation matrix on all combined variables using PROC REG with the collinearity diagnostics option (SAS Institute 1985) to eliminate intercorrelated variables. Interrelatedness can lead to switching of variables in a stepwise discriminant function analysis and to difficulty in interpreting the importance of predictor variables (Green 1979). Multicollinearity among regressors also results in unstable estimates and high standard errors (SAS Institute 1985). All variables with variance inflation factors (VIFs) of greater than 2.0 were removed from further analysis.

Table 2. CAPTURE data for 1989–90 livetrapping of *P. maniculatus*, Great Smoky Mountains National Park.

Sites	Year											
	1989						1990					
	Model	Number Captured	Population Estimate	SE	95% CI	P-hat	Model	Number Captured	Population Estimate	SE	95% CI	P-hat
Rooted:												
Lonely Spruce	M(h)	21	27	3.23	20–34	0.34						
Hogtrap	M(t)	19	20	1.07	17–23	0.38						
Sweat Heifer	M(o)	7	10	3.34	3–17	0.21	M(t)	12	12	0.01	11–13	0.54
Double Springs							M(o)	17	19	2.61	13–25	0.30
Indian Gap 2							M(o)	8	8	0.58	4–8	0.47
Mean			19.0					13.0				
SE			4.93					3.21				
Unrooted:												
Indian Gap 3	M(o)	6	7	1.55	3–11	0.30	M(t)	4	5	0.00	5–6	0.55
Indian Gap 1	M(h)	17	26	4.45	17–36	0.23	M(o)	11	11	0.84	9–13	0.45
Indian Gap 2	M(o)	22	23	1.55	19–27	0.49						
Beech Gap							M(o)	12	13	1.52	9–15	0.35
Mean			18.7						9.7			
SE			5.90						2.40			



We used PROC STEPDISC (SAS Institute 1985) to select remaining variables for construction of a discrimination model. The stepwise selection process was used with a significance level of variable entry into the model set at 0.15. We selected a moderate significance level in order to “choose the model that provides the best discrimination using the sample estimates” (SAS Institute 1985:750). We then analyzed variables selected for inclusion in the discrimination model using PROC DISCRIM (SAS Institute 1985) to test the assumption of homogeneity of the within-group covariance matrices and to generate a classification outcome. Significance level for the test of homogeneity was set at 0.05. We set prior probabilities proportional to sample sizes.

We used the Kappa statistic to measure the improvement of the classification rates over chance assignments. This statistic ranges from zero, which indicates no improvement in assignments, to one, which indicates perfect assignment (Fleiss 1973, Rexstad et al. 1988). Alpha level for this test was set at 0.05.

We used PROC CANDISC (SAS Institute 1985) on the variables selected by PROC STEPDISC to test separation of traps into successful and unsuccessful classifications and to obtain standardized canonical coefficients that suggest directional relationships between the selected variables and the two classifications. In an attempt to identify important microhabitat variables properly, we validated models by analyzing data from both years individually, and then compared the results. For each year's data, the discriminant function analyses identified significant variables that were associated with successful and unsuccessful traps.

## RESULTS

### MAMMALS

Populations of deer mice were low during both 1989 and 1990 (Table 2). Because population sizes were so small during both years, the models selected by CAPTURE did not perform well (Otis et al. 1978), and the estimates are likely biased with low precision (White et al. 1982). The two-way ANOVA performed on deer mouse population means pooled from both years revealed no significant differences: (1) between population sizes on rooted and unrooted sites ( $F = 0.18$ ,  $P = 0.68$ ), between the population sizes of 1989 and 1990 ( $F = 2.99$ ,  $P = 0.12$ ), or due to interactions between site class and year ( $F = 0.12$ ,  $P = 0.74$ ).

Table 3 summarizes all non-*Peromyscus* captures. Low capture frequencies prevented statistical analysis of any of these data.

Table 3. 1989–90 non-*Peromyscus* captures on rooted and unrooted sites, Great Smoky Mountains National Park. Totals listed by trap type.

Site	Species	Number
Rooted:		
Live trap	<i>Napaeozapus insignis</i>	5
	<i>Synaptomys cooperi</i>	1
	<i>Blarina brevicauda</i>	2
	<i>Mustela frenata</i>	1
Pitfall	<i>Sorex cinereus</i>	5
Unrooted:		
Live trap	<i>Napaeozapus insignis</i>	2
	<i>Blarina brevicauda</i>	1
	<i>Mustela frenata</i>	2 or 3 <sup>1</sup>
	<i>Clethrionomys gapperi</i>	1
Pitfall	<i>Napaeozapus insignis</i>	1
	<i>Sorex cinereus</i>	8
	<i>Sorex fumeus</i>	1
	<i>Synaptomys cooperi</i>	1

<sup>1</sup> No attempt was made to mark live weasels; therefore, two captures at one site could represent one or two individuals.

Table 4. Discriminant analysis between successful and unsuccessful traps in the capture of *P. maniculatus*, Great Smoky Mountains National Park, 1989–90. Variables are listed in order of entrance into the model.

Variable	Wilks' lambda	Probability < lambda	Standardized coefficient
1989			
% herb cover	0.93	0.0001	-0.57
% evergreenness	0.87	0.0001	-0.48
% canopy cover	0.83	0.0001	0.45
% star chickweed	0.81	0.0001	0.34
% spring beauty	0.79	0.0001	-0.34
% exposed rock	0.78	0.0001	0.24
1990			
understory distance	0.98	0.0276	-0.63
% canopy cover	0.96	0.0090	-0.73
% herb cover	0.94	0.0058	-0.50
% exposed rock	0.91	0.0020	0.43



## VEGETATION

Analyzing the 1989 data with PROC REG and then discarding all variables with VIFs above 2.0 eliminated all but 39 of the original 97 variables. PROC STEPDISC retained six variables for inclusion in the final model. These six variables, in order of entry into the model, included percent total herb cover, percent evergreenness, percent canopy cover, percent greater star chickweed, percent spring beauty, and percent exposed rock (Table 4).

The combined 1989 data set failed to meet the assumption of homogeneity between within-group covariance matrices ( $P = 0.0001$ ). PROC DISCRIM was programmed to use a pooled covariance matrix. The equality between within-group covariance matrices assumption is similar to the equal variance assumption of univariate analysis (Green 1979). For the 1989 data set, there was a significant difference ( $P = 0.0001$  for each) between the equality of within-group covariance matrices. Despite the failure of the data to meet the required assumption, we programmed PROC DISCRIM to use a pooled covariance matrix.

Our line of reasoning for this approach was the following. First, the test used by PROC DISCRIM is extremely sensitive to nonnormality and rejects too often (Dr. Thomas Gerig, Department of Statistics, North Carolina State University, personal communication). Second, many investigators believe that discriminant function analysis is robust and that the assumptions need not be strictly met (Johnson 1981, Taylor 1990). Third, we used linear discriminant analysis primarily as an exploratory tool and not a confirmatory tool (Williams 1983, James and McCulloch 1990). Fourth, our study had a relatively large number of observations and a large observation to variable ratio. Data from both years consisted of 216 observations (one set of observations per trap). During 1989, the ratio of observations to variables entered into the stepwise discrimination analysis was 30:1. In 1990, the ratio was 15:1. Rexstad et al. (1988) found that the median sample size of 28 multivariate studies published between 1985 and 1987 in *The Journal of Wildlife Management* was 99 observations and 12 variables, or an 8:1 ratio. Taylor (1990:188) stated that "relaxation of assumption is most justified with large data sets." However, some authors do caution that the assumption is important and should not be dismissed lightly (Williams 1983, Rexstad et al. 1990).

Classification success using this method was fair. Of the 102 unsuccessful traps, 66.7% were correctly classified as being unsuccessful. Of the 114 successful traps, 79.0% were correctly classified. The Kappa statistic indicated that these classification rates were

significantly different than zero ( $Kappa = 0.46$ ,  $P < 0.0001$ ). Standardized coefficients (Table 4) indicate trap success was directly related to percent canopy cover, percent greater star chickweed, and percent exposed rock, but inversely related to percent total herb cover, percent evergreenness, and percent spring beauty. The group centroid on the discriminant axis for successful traps (0.50) was significantly different ( $F = 9.74$ ,  $P = 0.0001$ ) from the group centroid of unsuccessful traps (-0.56). This suggests that the discriminant function could separate successful and unsuccessful traps based on the habitat variables under consideration.

We ran a series of one-way ANOVAs on the six variables that were included in the final model to determine if these variables could separate rooted and unrooted sites (Table 5). None of the six variables was significantly different between rooted and unrooted sites.

In 1990, the multicollinearity test revealed that no variables had to be removed from the analysis because of interrelatedness. PROC STEPDISC chose five variables for the model (in order of entrance): distance to closest understory tree, percent canopy cover, percent total herb cover, percent spring beauty, and percent exposed rock (Table 4). As compared to the 1989 model, one new variable (understory tree distance) was added and two variables (percent evergreenness and percent greater star chickweed) were deleted. We removed percent spring beauty from further analysis because of a scarcity of observations that resulted in a covariance matrix that

Table 5. ANOVAs to separate rooted and unrooted sites, Great Smoky Mountains National Park, performed on variables chosen by discriminant analysis (Table 4).

Variable	Rooted mean	Unrooted mean	<i>F</i>	<i>P</i>
1989				
% herb cover	1.18	1.13	0.16	0.71
% evergreenness	0.04	0.21	4.04	0.11
% canopy cover	0.99	1.09	3.84	0.12
% star chickweed	0.17	0.13	0.34	0.59
% spring beauty	0.001	0.02	0.84	0.41
% exposed rock	0.04	0.003	4.19	0.11
1990				
understory distance	1.38	1.45	0.08	0.79
% canopy cover	1.01	1.07	0.73	0.44
% herb cover	0.88	0.94	0.32	0.60
% exposed rock	0.01	0.008	0.12	0.74



was not a full rank and therefore could not be properly analyzed by PROC DISCRIM.

PROC DISCRIM revealed that the 1990 data also failed to meet the assumption of equality between within-group covariance matrices ( $P = 0.0008$ ). As was done for 1989 data, we ran PROC DISCRIM with a pooled covariance matrix. Results of this classification were almost as good as in 1989. Of the 139 unsuccessful traps, 61.0% were correctly classified. The Kappa statistic indicated that classifications were also significantly different from zero (Kappa = 0.26,  $P < 0.0001$ ). Standardized coefficients (Table 4) indicated that trap success was directly related to percent exposed rock and inversely related to percent canopy cover, percent total herb cover, and distance to closest understory tree. These relationships are similar to the previous year's except that in 1989 percent canopy cover was directly related to trap success. The group centroid on the discriminant axis for successful traps (0.36) was significantly different ( $F = 3.93$ ,  $P = 0.004$ ) from the centroid for unsuccessful traps (-0.20).

None of the 1990 variables was significantly different between rooted and unrooted sites (one-way ANOVAs, Table 5).

## DISCUSSION

### MAMMALS: POPULATION TRENDS

Our findings are in agreement with Singer et al. (1984) that there was no significant difference in populations of deer mice between rooted and unrooted sites. We believe that the semi-arboreal habits (Wolff and Hurlbutt 1982, Singer et al. 1984), choice of food items (Howe et al. 1981, Linzey and Linzey 1973), and generalist nature (Baker 1968) of deer mice allow them to quickly adapt to or not be affected by hog rooting disturbances. Although we did not capture enough shrews or voles to allow a quantitative comparison, their presence on rooted sites indicates that populations of these mammals are not permanently extirpated from rooted areas and that they may recolonize disturbed areas quickly.

### VEGETATION: MICROHABITAT SELECTION

One problem all habitat studies of this type face is the assumption that the reason a particular habitat is unused is that the habitat in that area is unsuitable for the animal (Johnson 1981, James and McCulloch 1990). However, habitat might not be used simply because of low population size. Our classification rates were probably lowered by this circumstance because mouse populations at some sites were extremely low.

Validation of the discriminant analysis models by replication of the study is highly recommended (Taylor 1990), but proper approaches to validation are usually not performed in wildlife habitat studies (Rexstad et al. 1990). One advantage of our study is that we had two years of data, and thus we attempted to confirm the importance of variables selected by the discriminate function analysis. Of the three variables that appeared in both years and that produced standardized coefficients, percent herb cover was inversely related in both years, percent exposed rock was directly related in both years, and percent canopy cover was directly related in one year and inversely related the next.

The failure of the ANOVAs to detect any significant difference between microhabitat variables at rooted and unrooted sites confirms what is to be expected. Assuming deer mice are selecting certain microhabitat features as preferred habitat, and if there are no differences in mice populations between rooted and unrooted sites, then it seems reasonable that there would be no differences in the key microhabitats between rooted and unrooted sites.

It is difficult to compare our research with other discriminant analysis studies of small mammal habitat because the majority of other studies concentrated on separating the preferred habitat of two or more small mammal species within a homogeneous or heterogeneous habitat (Dueser and Shugart 1978, Kitchings and Levy 1981, Vickery 1981, Buckner and Shure 1985). We feel that our study is unique in that it focuses on the use of discriminant analysis to predict trap success for one species within a generally homogeneous habitat type.

Two microhabitat variables appeared in both the 1989 and 1990 overall models and maintained the same directional relationship both years. Therefore, these variables seem to be particularly important to deer mice. Mice seem to be more likely to orient toward traps with greater exposed rock in the area and less herbaceous cover. Open areas very close to the ground, as the result of exposed rock and thin ground cover, would provide deer mice with a wide view of the terrain. This open view might be advantageous to the mice for two reasons. First, perhaps foraging would be facilitated in that seeds, fruits, and insects would be more visible. Second, the open ground could make it easier for mice to detect and avoid terrestrial predators such as the long-tailed weasel (*Mustela frenata*). Open ground cover would not necessarily expose foraging mice to avian predators if the midstory was thick enough to compensate.



The understory distance variable is perhaps the easiest to confirm and interpret. Trap success decreased as distance to understory trees increased, which might be a reflection of available refuges or a measure of midstory canopy. Vickery (1981) found that deer mice used areas with heavy midstory cover which may be related to predator avoidance. The heavy midstory would provide cover from aerial predators while at the same time providing closely accessible escape routes from terrestrial predators. Lockard and Owings (1974) hypothesized that bannertail kangaroo rats (*Dipodomys spectabilis*) seasonally vary foraging patterns to avoid exposure on moonlit nights because of increased predation pressure. The preference of deer mice for a heavy midstory cover, coupled with the importance of a wide view at ground level, suggest a habitat preference that allows protection from both terrestrial and aerial predators while at the same time providing optimal foraging opportunities.

The inverse relation of trap success to percent evergreenness agrees with the findings of Kirkland and Griffin (1974) that deer mice avoid coniferous areas. Most of the individual trap sites with a high ratio of evergreenness were located near the edges of the trap grid where beech forest faded into spruce-fir forest. The appearance of percent evergreenness as an important variable probably represents marginal deer mouse habitat. Avoidance of these areas may be related to the preference of the more dominant *Clethrionomys gapperi* (Crowell and Pimm 1976) for coniferous areas in the Great Smoky Mountains National Park (Linzey and Linzey 1971). Competition may be a factor in microhabitat selection only along the fringes of primary deer mouse habitat.

Other variables in the models are difficult to interpret. It is doubtful that the presence of spring beauty is of any biological importance. This vernal herb was very difficult to detect, and the few times it was detected it did not seem to be contributing anything to the habitat requirements of the mice. Greater star chickweed is a fairly ubiquitous herb in the beech forests, and there is no obvious explanation for its appearance as a variable. Perhaps, chickweed had set seed by our trapping dates, thus mice were orienting toward this plant as a food source. We have no ready explanation as to why these variables appeared in the model.

Neither can we offer an explanation for canopy cover being directly correlated to trap success one year and inversely correlated the next. This might simply be a stochastic artifact, or it could be related to the nature of the statistics themselves. Dr. Gerig (personal communication) stated that it was not surprising that a variable appearing in one year's analysis might switch signs if it appeared

in another year's analysis and if the suite of variables with which it was found had changed even slightly.

#### FUTURE RESEARCH

Our data indicate that deer mice populations are not significantly affected by hog disturbance in the beech gaps. It is not clear, however, if this is because hog rooting does not disturb microhabitats important to the mice or because the mice are such generalists that they easily adapt to microhabitat changes. Future studies comparing food selection or home range use of mice in rooted and unrooted areas might help to clarify this question.

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# Notes on Post-breeding American Swallow-tailed Kites, *Elanoides forficatus* (Falconiformes: Accipitridae), in North Central Florida

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**ABSTRACT**—In 1982 we made observations and collected a limited sample of American swallow-tailed kites (*Elanoides forficatus*) summering in central Florida. Birds occurred in estimated densities of about three adult kites per kilometer of river. Post-breeding birds had heavy accumulations of subcutaneous fat. Adult males ( $n = 4$ ,  $\bar{x} = 550$  g) weighed less than females ( $n = 5$ ,  $\bar{x} = 613$  g), but more than immatures ( $n = 2$ ,  $\bar{x} = 481$  g). Mean mercury loads were 0.09 ppm for muscle, 0.25 ppm for liver, and 0.31 ppm for kidney tissues. All adults were actively molting flight feathers, making it possible to visually census for adult/young-of-year ratios in mid-July. Most food items were small flightless insects (8–50 mm), apparently gleaned from flower heads of cabbage palmettos. Major prey items consisted of various bugs: palmetto weevils (*Rhynchophorus cruenlatus*), horntails (*Eriotrenex formosanus*), queen fire ants (*Solenopsis invicta*), and young flightless grasshoppers (*Melanoplus* sp.). Several larger prey items—one green treefrog (*Hyla cinerea*) four anoles (*Anolis carolinensis*), and one bat (*Pipistrellus subflavus*)—were also recovered.

Examination of recent records of birds north of their current breeding range indicates that the main period of northward dispersal is mid-April through June, a period when nesting is in progress. Thus, these individuals probably represent young nonbreeding birds. After the mid-March to late June nesting season, local birds gather in small flocks, complete their molt, and move to larger communal summer roosts. By mid-August to early September, the kites depart for their South American wintering grounds.

The reduced breeding range of the American swallow-tailed kite is difficult to explain in view of the information obtained in our study. Our work suggests that the species is a feeding generalist and that it does not feed high on the food chain.

While the breeding biology of American swallow-tailed kites (*Elanoides forficatus forficatus*) has been examined in some detail (Synder 1974), other aspects of this bird's life history are described, for the most part, as scattered notes. This information has been

summarized by Bent (1937) and Robertson (1988). Skutch (1965) reports on nesting activities and feeding habits of the South American race *E. f. yetapa*. Other than nest biology studies, little recent information on this kite has been published, and that which has is limited mostly to reported occurrences of individual birds at interesting sites (i.e., Gross 1958) or dates (Hicks 1955). Millsap (1987) provided important information on pre-migration staging in South Florida. In this article, we provide information on the post-breeding biology of this bird and comment on its relationship to the phenology and conservation status of the species.

### STUDY AREA

Between 13 and 21 July 1982 we surveyed the St. Johns River by houseboat from the outlet of Lake Monroe near Sanford, Seminole County, downstream (north) to Black Creek near Orange Park, Clay County, Florida. Side excursions into major tributaries were made into Lake Dexter, parts of Murphy Creek, Dunns Creek, Crescent Lake, and Black Creek. We surveyed 252 km of the St. Johns River, its tributaries, and connected lakes, with some areas being resurveyed on the return trip. Width of the river varied from 100 to 200 m upstream to 6.5 km near Orange Park. Some of the lakes in the river were much wider (up to 10 km on Lake George). This entire stretch of the river was largely undeveloped on one or both banks.

The St. Johns River is bordered largely by river swamp communities, particularly on the west bank, which is lower in elevation than the east bank, and on most of the islands in the river. Portions of the east bank that are higher and better drained have more upland communities such as mesic hammocks. The swamp forests are frequently flooded by a combination of high water, wind, and tidal action. Trees dominating the river swamp communities are bald cypress (*Taxodium distichum*), swamp tupelo (*Nyssa sylvatica*), water locust (*Gleditsia aquatica*), water ash (*Fraxinus pauciflora*), red maple (*Acer rubrum*), water hickory (*Carya aquatica*), and cabbage palm (*Sabal palmetto*). A characteristic shrub layer of button-bush (*Cephalanthus occidentalis*), willow (*Salix longipes*), palmetto (*Sabal minor*), and wax myrtle (*Myrica leriiferus*) densely lines the river, but is less conspicuous in the swamp interior.

Inland the swamp forests are typically bordered by a hydric hammock community—a transition between the swamp and upland communities. Where topographic change is gradual, transition zones between habitats are poorly defined. Trees common in this community include swampbay (*Persea pubescens*), water oak



(*Quercus nigra*), sweet gum (*Liquidambar styraciflua*), loblolly-bay (*Gordonia lasianthus*), cabbage palm, Florida elm (*Ulmus floridana*), and longleaf pine (*Pinus palustris*). Shrubs and vines are prominent, and herbaceous vegetation is sparse. These two communities in many cases extend for several kilometers from the river's edge.

## METHODS

Individual kites and flocks of soaring kites were photographed. We studied these images for molt sequence. Small images were enlarged so that feather details of individual birds were obvious. Some individuals may have been photographed several times, but the photographs were taken at a number of locations over a 7-day period, so it is clear that most images represent different individuals. The photographs are catalogued in the North Carolina State Museum of Natural Sciences' collection of bird photographs.

We collected specimens with a 12-gauge shotgun while birds were in flight. Gizzards were preserved in 25% formaldehyde and were later examined for prey items. Three specimens were frozen and were later thawed for analysis of mercury loads in muscle, liver, and kidney tissues as per methods outlined by Stoneburner and Harrison (1981). The specimens are in the collection of the North Carolina State Museum of Natural Sciences (NCSM).

We examined 75 study skins in major North American collections for additional information on age and molt. Data from museum collections allowed us to illustrate the documented egg dates for the species in Florida. Information on vagrants found north of their current breeding area was compiled from various sources, but data are from dates after extirpation of the species from the northern portion of their range.

## RESULTS AND DISCUSSION

Because swamp forests such as those bordering the St. Johns River appear to be the preferred habitats for these kites, and the habitat is duplicated throughout much of central Florida, it seems likely that we were observing local resident birds. Along the same lines, examination of stomach contents (see below) did not indicate that birds were converging from great distances to opportunistically feed on some locally abundant prey species.

Apparently this area has been used by nesting swallow-tailed kites for a long time; there are 12 egg collections from San Marito, Putnam County from between 1887 and 1895 in various North American museums.

*Density and age ratios*—On the 7 days of our field study, 200–250 swallow-tailed kites were seen along a 252-km stretch of

the St. Johns River. Evening counts of flying, pre-roosting adult kites which could be distinguished from younger birds (see below) suggested an average of one adult per kilometer of river, but all sightings were in the upper reaches where the river channel was the narrowest and the swamp forest best developed. Density calculations for just the upper reaches indicated there are about three adults per kilometer of river north of Lake George. This calculation does not account for secondary tributaries or additional kilometers of river frontage created by islands. There is a strong probability of additional flocks away from the main river or small flocks which were not detected.

Interestingly, very few young kites were observed. Only 2 of the 12 collected birds were immatures, and these were selectively collected because of plumage differences in our sampling bias that favored nonmolting birds. Of 142 individual bird images on photographs (Fig. 1), 61 (43%) were too far away or angled in such a way that molt, if present, could not be seen. Of the remaining 81 images, 84% were adults in molt, and 16% were young-of-the-year.

*Food and feeding habits*—Although there is a considerable amount of literature on feeding of swallow-tailed kites, much repeats Audubon's (1840) observations or comments on large, spectacular prey items noted in field observations. Swallow-tailed kites did not come under the attention of the food habit studies of the early portion of this century (i.e., McAtee 1935). Skutch (1951, 1965) and other mention that swallow-tailed kites were seen plucking young birds from nests, and Skutch (1965) and Haverschmidt (1962) provide firsthand accounts of the importance of insects in the diet of South American birds. Bent (1937:49–50) summarizes the observations of Audubon and others on food and feeding habits; he adds "its food includes small snakes, for which it is often called 'snake hawk,' lizards, frogs, and tree toads. It feeds very largely on grasshoppers, locusts, crickets cicadas, beetles of various kinds, bees, wasp grubs, dragonflies, cotton worms and various other insects." Unfortunately, Bent did not indicate how this documentation was obtained. Presumably it was from a combination of data compiled from specimen labels, correspondence, and literature; but the size of the series examined and the geographic area and season taken are unknown. In our examination of museum specimens we found only two references to prey items on specimen tags "*stomach contents* - grasshoppers, crickets, etc." (AMNH 352039, Georgia, Richmond Co., 21 July 1900, adult, female) and "*stomach contents* - grasshoppers and beetles" (AMNH 352038, Georgia, Richmond Co., 23 July 1890, adult, male). Robertson (1988:130) summarizes



**A****B****C**

Fig. 1. Photographs of American swallow-tailed kites (*Elanoides forficatus*) taken July 1982 near Sanford, Seminole County, Florida. A. Enlarged portion of flock of kites; B. Enlargement showing no indication of molt of flight feathers (assumed first year bird); C. Enlargement showing gaps in flight feathers and asymmetrical tail feathers of adult.

literature on the food habits of this species and notes that the bird was apparently "more insectivorous in its former central U.S. range taking more vertebrate prey in the south." However, much of the information obtained in the Southeast, and all recent information, is from observations at nests where adults regularly bring vertebrate prey. If small insects are brought to nestlings as food items, they would be difficult to detect by observing the birds from blinds.

Only two of the birds that we collected were actively foraging. A single adult female, collected on 16 July, was seen in aerial pursuit of a small flying insect. This bird was one of a few seen over the river in the morning (1020 hours) and one of the few solitary birds we encountered. Its stomach contained only fragments of beetles (Coleoptera). The remaining birds were all collected late in the afternoon, before roosting, and had extremely full stomachs. Another foraging individual, an immature, was col-

Table 1. Food items recovered from gizzards of eight swallow-tailed kites, St. Johns River, Florida, 1982.

Food Items	Number of Individuals	% of Total	Frequency of Occurrence	Length of Food Items (mm)
Cicada ( <i>Tibiceu</i> sp.)	4	1	2	40-50
Cicada (Cicadidae)	1	<1	1	20
Palmetto weevil ( <i>Rhynchophorus cruenlatus</i> )	44	13	8	20-31
Horntail ( <i>Eriotrenex formosanus</i> )	21	6	5	25-30
Wasp	1	<1	1	30
Leaf-footed bug (Coreidae)	66	19	6	25 +
Grasshopper ( <i>Melanoplus</i> )	146	42	4	18-25
Wheelbug ( <i>Arilus cristatus</i> )	5	1	3	25 +
Assassian bug (Reduviidae)	2	<1	1	25
<i>Cotinis</i> sp.	5	1	4	25
Shield-backed bug (Scutellerinae)	3	<1	1	20-25
Stink bug ( <i>Podisus</i> sp.)	4	1	1	20
Pentatomidae	11	3	1	20
Bee (Apoidae)	1	<1	1	20
Cricket (tree or brush) (Gryllidae)	1	<1	1	20
Imported fire ant ( <i>Solenopsis invicta</i> )	21	6	6	8-10
Cerambycid beetle ( <i>Clytus ruriocla</i> )	4	1	3	
Spider (Araneae)	1	<1	1	20
Mite (Acarina)	1	<1	1	0.1
Bat ( <i>Pipistrellus subflavus</i> )	1	<1	1	
Anole ( <i>Anolus carolinus</i> )	1	<1	1	
Tree frog ( <i>Hyla cineria</i> )	1	<1		
Total	345			



lected on 15 July. At about 1800 hours it descended from a flock of 15–20 birds soaring above the canopy of the swamp forest adjacent to the river and made repeated passes at some tangled branches hanging over the river. The bird would glide into the area, reach out for prey items with its talons, miss, glide out over the river, circle up over the sites, and glide back to repeat the attempted catch. We did not see the prey item. This behavior was repeated at least four times before the bird was collected. The stomach contained three adult Carolina anoles (*Anolis carolinensis*), various beetles, and true bugs.

We examined the stomachs (gizzards) of all 12 birds collected for food items. The two described above and one other individual were examined only superficially in the field. The stomachs of the remaining nine birds were preserved in formalin. Eight were examined later (Table 1), and one was lost. Mass of individual stomach contents ranged from 11.7 to 47.8 g, and by volume each contained 10–62 mL of food. Based on the degree of digestion, the bat was probably eaten the evening before the bird was collected. It would be interesting to know if the bat was captured while it was roosting or in flight because Pipistrells often emerge before dark.

Insects represented the bulk of the diet. Those consumed varied between 8 and 50 mm in length, whereas the majority were between 20 and 30 mm long (Fig. 2). Several of the prey organisms are flightless, many do not fly regularly, and some were in immature stages (grasshoppers [Acrididae], bugs) which were not yet capable of flight. We surmised that the majority of feeding activity consists of capturing prey from the tree tops or shrubs, by repeatedly swooping in vegetation until prey is flushed, or a combination of these two methods. The presence of palmetto weevils (*Rhynchophorus cruenlatus*) in all stomachs we examined indicates that a large percentage of feeding is done in the crowns of cabbage palms, a tree common in the higher portions of river swamp forest. The presence of wheel (*Arilus cristatus*) and assassin bugs (Reduviidae), a bee, and several other insects suggests that the kites may have been foraging around the flowering stalks of the palmettos. A local resident reported seeing on several occasions kites repeatedly flying around the tops of these palms. Percentages for major prey items we identified are shown in Figure 3.

Snyder (1974:91) reports two types of foraging behavior: talon-grabbing of resting prey from the outer leaves and branches of trees, and captures of flying prey “so effortless that it did not ever appear to disturb the soaring pattern of the bird.” Observations of

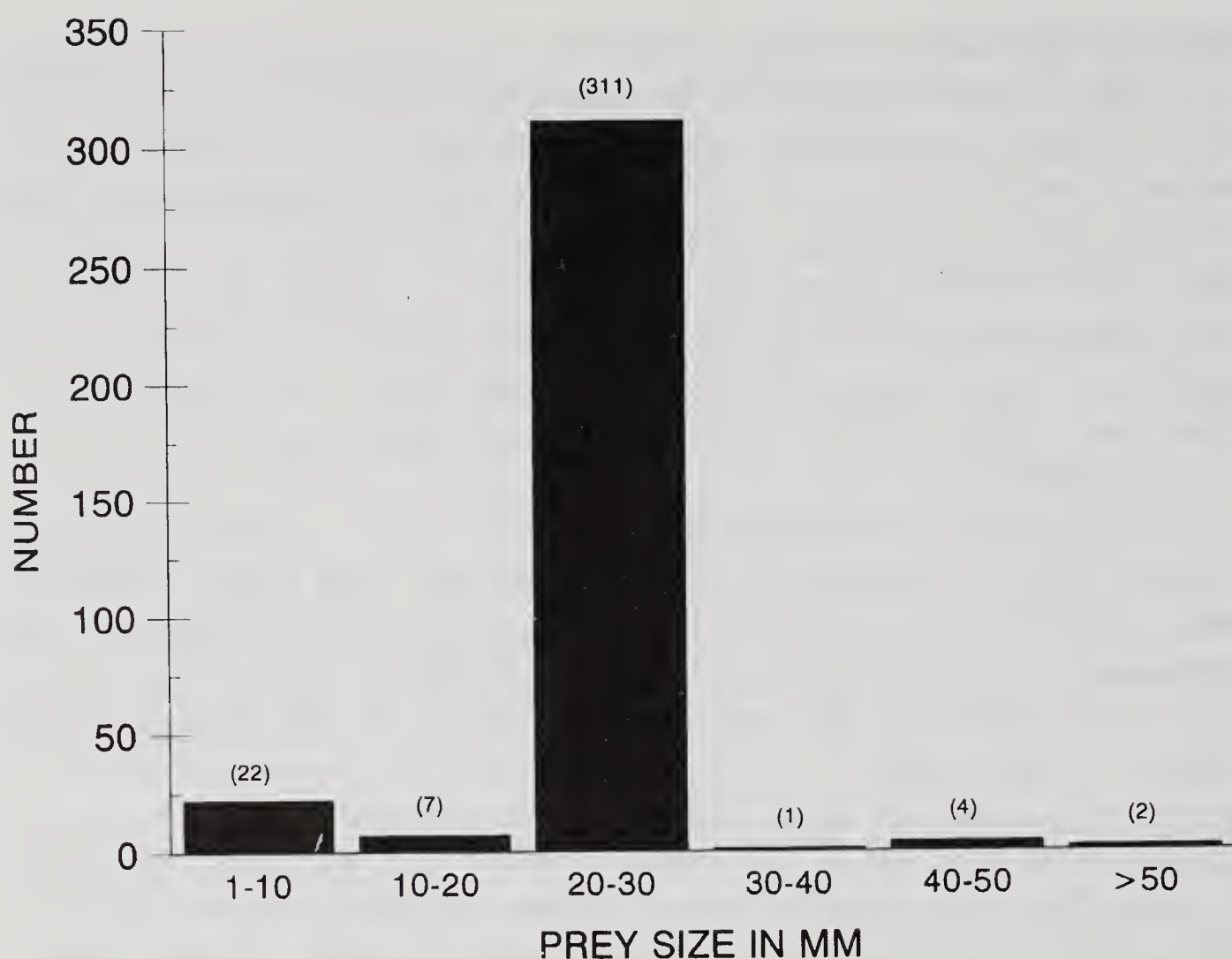


Fig. 2. Prey size of food items recovered from the stomachs of eight American swallow-tailed kites (*Elanoides forficatus*) based on 345 identified items.

earlier workers and our observations suggest that all feeding is certainly done on the wing.

Popular accounts of swallow-tailed kites feeding emphasize aquatic snakes and dragonflies as important food items. Synder's (1974) observation of prey items brought to nests by parents is one of the few systematic treatments of feeding and food habits. He observed that very few insects were brought to the nest, and the most conspicuous food items were anoles, hylid frogs, and nestling birds. Nevertheless, Synder (1974:91) noted that he "often observed adults hawking insects and believed that such food may form a significant fraction of adult diet." It is interesting that although we saw many genera of dragonflies in great abundance along the St. Johns River, none was recovered as prey items in the stomachs of birds we collected.

Most of the food items in Table 1 were certainly not captured when the prey items were flying. A possible exception is the imported fire ant (*Solenopsis invicta*), as all individuals recovered were winged queen ants. Queen fire ants are capable of flight and could easily have been captured while flying, although exhausted ants



could have been gleaned while resting. Although these ants are only 8-mm long, they may represent a major food source. Morrill (1974) studied imported fire ants in several habitats in northern Florida and found that emergence of alates averaged 187,000/acre/year (75,700/ha/year). The heaviest flights occurred between April and August, indicating that they could be an important food source throughout most of the kites' period of summer residence. Haverschmidt (1962) noted that the gizzard of one kite (*E. f. yetapa*) collected in Surinam was full of flying ants.

The recovery of 21 individuals of *Eriotremex formosanus*, a horn tail, in five of the stomachs is of interest entomologically. This is an exotic species, and these individuals represented the first examples found east of Louisiana (J. Green, North Carolina Department of Agriculture, personal communication).

Mercury analysis of body tissues indicated that these birds are not receiving much mercury in their diets. This is probably indicative of the intermediate trophic level of this species. Mean mercury loads for three adults of the series collected were 0.09 ppm for muscle, 0.25 ppm for liver, and 0.31 ppm for kidney tissue. The higher concentrations for liver and kidney tissue in the kites suggest that the birds are successfully regulating (excreting) mercury. Comparisons of various seabird species we examined at the same time and with the same methods show high mercury loads (0.23–98 ppm for muscle, 0.61–60 ppm for liver, and 0.34–26 ppm for kidney) (P. Whaling and D. Lee, unpublished data).

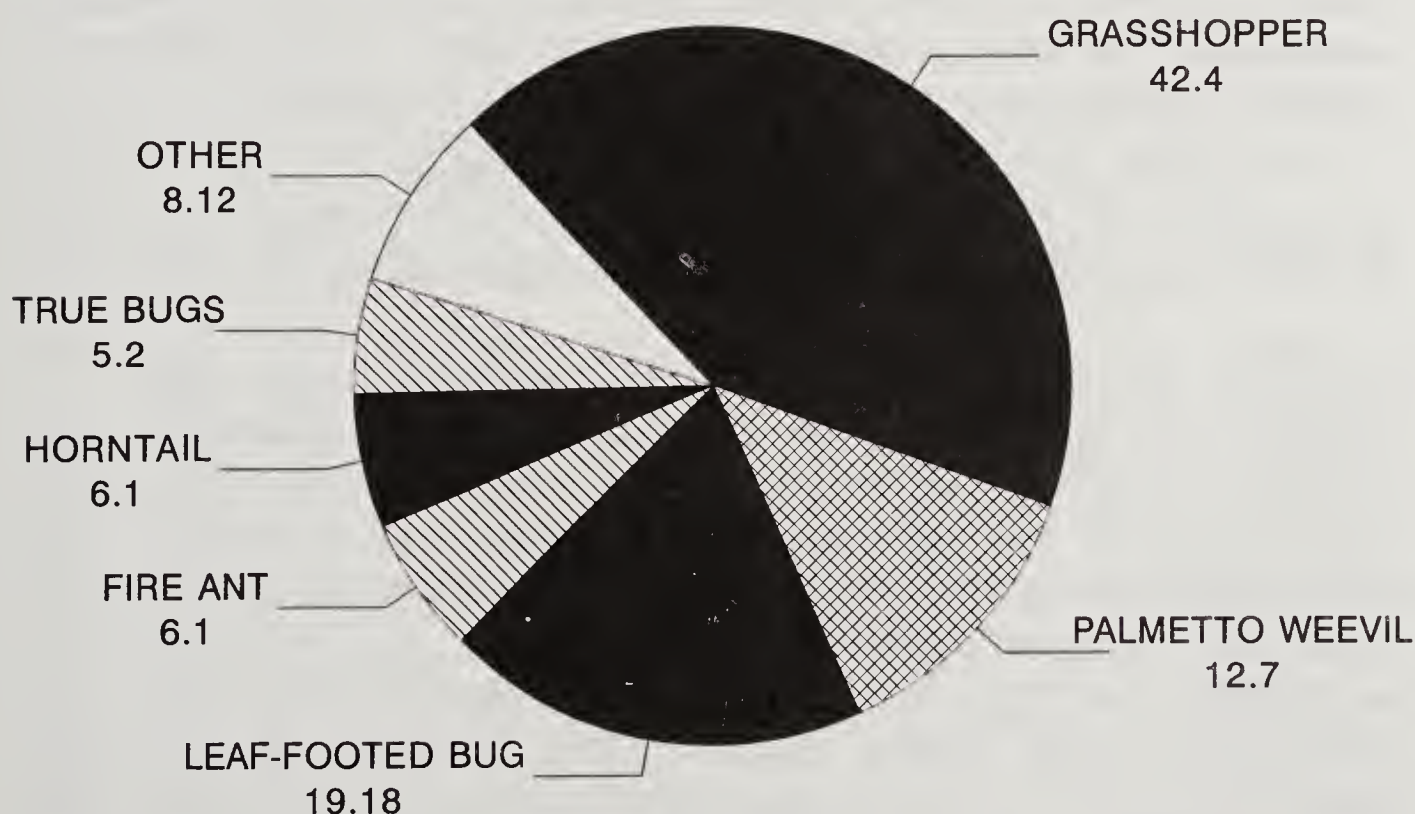


Fig. 3. Percentages of major prey types recovered from eight swallow-tailed kites, *Elanoides forficatus* collected in July 1982.

*Body mass*—Little information is available on masses of swallow-tailed kites, and examinations of museum labels indicates that few specimens in collections contain mass information. For example, Dunning (1984) found reference to only two unsexed swallow-tailed kites that weighed 445 and 504 g for his monograph on body masses of North American birds, and Robertson (1988) cited only five recorded masses for the North American race. Of the 75 birds we examined in museum collections, we found only two with information on mass (see below). Of the series we collected, four adult males averaged 550.6 g (range = 520.0–576.1), and five adult females averaged 613.0 g (range = 551.0–654.5).

The heavier masses of adult females compared to adult males corresponds with the sexual size dimorphism already documented for the species (Friedmann 1950). Immature birds weighed less than adults (2 males  $\bar{x}$  = 481 g, range = 459–503 g). John Cely (South Carolina Wildlife and Marine Resources Department, personal communication) provided information on masses of six birds he followed in telemetry studies in South Carolina. The one of known sex was a female that weighed 510 g. The other five adults (sex unknown) weighed 440–502 g ( $\bar{x}$  = 471.4). Males from south Florida weighed 475 and 422.7 g (Robertson 1988).

Table 2. Molt of primary feathers on 11 swallow-tailed kites collected on the St. Johns River, Florida, July 1982. All from this study except the American Museum (AMNH) specimen, which is from the same general locality and was collected on 14 July 1877. Feather condition, O = old, S = in sheath, N = new.

NCSM	Primary Numbers									
	10	9	8	7	6	5	4	3	2	1
male 8521	O	O	O	O	O	O	O	O	S	N
male 8525	O	O	O	O	O	O	O	O	S	S
male 8527	O	O	O	O	O	O	S	N	N	N
male 8502	O	O	O	O	O	O	O	N	N	N
female 8523	O	O	O	O	O	O	O	O	O	S
female 8479	O	O	O	O	O	S	N	N	N	N
female 8522	O	O	O	O	O	O	O	O	N	N
female 8504	O	O	O	O	O	O	S	N	N	N
female 8503	O	O	O	O	O	O	O	N	N	N
female 8526	O	O	O	O	O	O	O	N	N	N
female (AMNH 352031)	O	O	O	S	S	N	N	N	N	N



Three specimens provide some insight into extreme and normal masses. One female found live with a broken wing on 14 May 1981 in Monroe County, Florida, died in captivity the same day and weighed only 331.5 g (MSB 9080). An adult female found dead in Bermuda on 17 March 1957 weighed 354 g (AMNH 788956). In our survey one adult female collected while it was feeding late in the afternoon weighed 485.5 g and had no accumulation of subcutaneous fat. With the exceptions of the one female mentioned above, all of the birds we collected in 1982 had heavy to very heavy subcutaneous deposits of fat. The fat buildup is probably related to fall migration. Perhaps fall migratory fat reserves were just starting to develop when we surveyed the population.

*Molt*—Based on his examination of five birds collected in August, Bent (1937) believed that swallow-tailed kites do not molt flight feathers until after the birds leave for their wintering areas. Robertson (1988) had no additional information but noted that individuals had been seen in south Florida and Costa Rica lacking remiges and rectrices as early as late May.

We found all adults along the St. Johns River to be in active flight feather molt in July. The birds all had new flight-feathers or feathers in sheath on the inner-most primaries, and the outer-most six to ten were old. At the time we collected the birds, feathers one to five were replaced or were being replaced (Table 2). Females appear to be slightly more advanced than males in feather replacement. In addition to the series collected, flight feather replacement is also apparent from photographs taken of birds in flight during the same period. Molt of tail feathers was also obvious on specimens obtained and from analysis of photographs. The new tail feathers were quite advanced in development, but replacement or feather growth was not symmetrical, and right and left forks of the tails were different lengths. Young-of-the-year birds exhibited no molt.

Only a few specimens of adult swallow-tailed kite skins that were examined from other places and dates showed any indication of molt. Thus, the total replacement of flight feathers is likely completed very rapidly after the nesting and fledgling season. Probably the entire process is typically completed between late June and the end of July. However, some Florida birds might still be in wing molt in mid-August. One adult female specimen collected on 18 July 1899 (AMNH 352035, Marco Island, Florida) had completed molt and had all new flight feathers. A 17 July 1988 adult female (AMNH 469954, Chatham Bend River, Florida) had completed its primary molt and had replaced all but the outer two tail

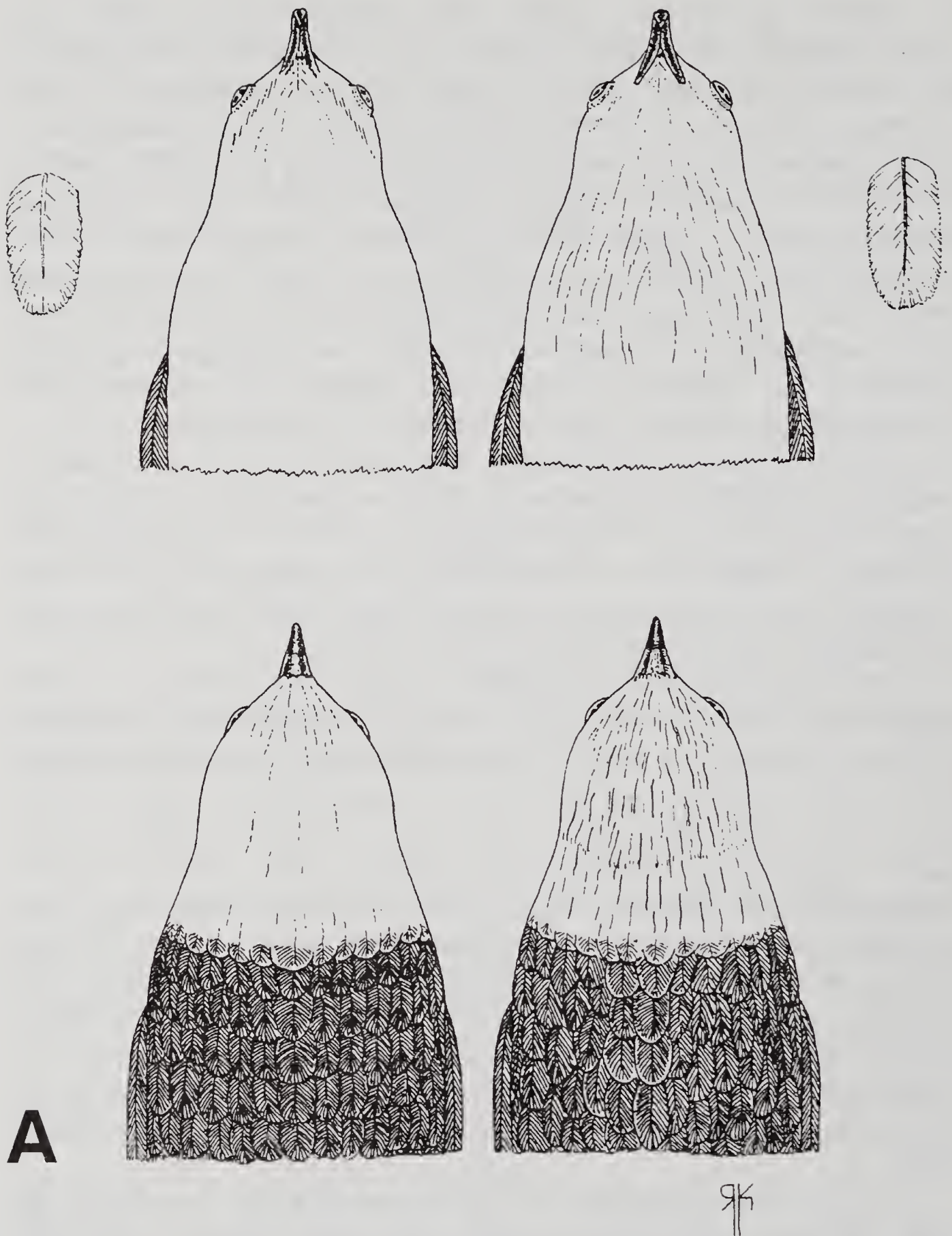


Fig. 4. Plumage comparison of adult (NCSM 8479, female) and young-of-the-year (NCSM 9988, male) American swallow-tailed kites (*Elanoides forficatus*). Specimens from July 1982, St. Johns River, Florida; A. Top ventral aspect left adult, right young-of-year. Bottom dorsal aspect, adult on left. Streaking on head and neck of young-of-year is caused by tan feather shafts. The occasional dark feather shafts on adult are black. B. Dorsal feathers of adult (left) and young-of-year. Feathers of young are white edges, whereas new feathers of adult lack white edges.







feathers. An adult female from 21 July 1900 (AMNH 352039, Richmond County, Georgia) still had two old outermost tail feathers, and all others were new. The primaries were also new. An adult male collected on 23 July 1890 (AMNH 3520 38, Richmond County, Georgia) had primaries 1–4 new, the outer 7–10 were old, and 5 and 6 were in sheath. An adult male from 14 July 1877 (AMNH 352031, St. Johns River, Florida) still had its old tail feathers, but new ones were coming in, primaries 6 and 7 were growing, and 1–5 were new. Adult specimens from January ( $n = 3$ ), February ( $n = 2$ ), March ( $n = 8$ ), April ( $n = 9$ ), May ( $n = 9$ ), and June ( $n = 3$ ) showed no signs of molt. Those from August ( $n = 6$ ) and November ( $n = 1$ , captive UF11256) had all new feathers (specimens from various museums and various localities, individuals from January and February were *E. f. forficatus* from Central and South America). Based on the lack of molting birds (from specimens or photographs) from months other than July and August, we assumed that young-of-the-year molt their flight feathers the following year at the same time as adults. We found no other molt evidence except for the specimens and photographs reported here. Robertson's (1988) comments on birds which were seen in late May with missing flight feathers would appear to be just that and probably do not represent a molt sequence.

*Northward dispersal*—Rapp (1944) examined 33 records of American swallow-tailed kites from the northeastern states (south through Pennsylvania) and concluded, based on four specimens, that (1) these birds did not represent the South American race, *E. f. yetapa* (this race is not an obligate long-range migrant), (2) there was no relationship between sun spots and northward movement of kites, and (3) there was no relationship between occurrence records and tropical storms.

After examining 143 records gleaned from the literature for states north of the species' current breeding range, we found the main period of occurrence to be mid-April through June (78% of total records). The largest number of records is in May (42%), a time when nesting activity is in progress in all portions of the breeding range of the North American subspecies. Thus, the northern occurrence records are probably of young nonbreeding birds. Bent (1937) reports egg dates of March 10 to May 18 for 81 records from Texas to Florida. Examination of Florida egg set data from various museums shows eggs from 10 March to 19 May with a reproductive peak in mid-April ( $n = 120$  egg sets).

Robertson (1988) believes that this kite reproduces in its first year based on three "adult" spring birds which retained some juve-



nile plumage characters. Based on museum skins, we could not identify plumage differences between post-hatching year and older swallow-tailed kites in the spring after they return from wintering areas. Age of post-breeding-season birds and their distribution, however, could be documented. Young-of-the-year individuals can be recognized by their generally duller plumage, by the finely streaked (tan colored feather shafts) neck and upper breast, and by the narrow white edge on the wing, wing covert, and tail feathers (Fig. 4). This white edging likely wears away quickly. Young birds also lacked the bloom of the adults, but the bloom does not hold up well on museum specimens. Furthermore, because adults are in active molt in July, it is possible to distinguish young-of-the-year birds from older ones when the birds are in flight. Observers are encouraged to report plumage and molt (or lack of molt) for July–August sightings. This information would help considerably in assessing population size and age structure. Unfortunately, at this time, museum specimens and literature records offer no concrete information to clarify differential movements of various age classes.

*Present and former distribution*—In view of the generalized diet of swallow-tailed kites and the wide dispersal of non-nesting individuals, it is difficult to explain the marked contraction of the breeding range of the species. Formerly these kites nested throughout much of the Mississippi drainage north to Oklahoma, Kansas, Nebraska, northwestern Minnesota, and southern Wisconsin. Ridgway (1895) stated that swallow-tailed kites were once common in Illinois. Parmalle (1958) reported a complete femur of this species from a Middle Mississippian Midden (1200–1500 AD) in Madison County, Illinois, and Goslin (1955) had zooarchaeological evidence for this species from rock shelters used by Indians in Ohio, suggesting that in recent times the interior breeding range may have been larger than what was documented by early naturalists. Pearson et al. (1942) suggested that swallow-tailed kites nested on the Atlantic Coastal Plain north to North Carolina, and while North Carolina is generally regarded as the northernmost nesting area in the East (AOU 1982), there are no actual nesting records north of South Carolina. Presently the breeding range is restricted to the lower Gulf Coastal Plain and the Outer Atlantic Coastal Plain north to coastal South Carolina. While the decline and abundance of the snail kites (*Rostrhamus sociabilis*) in North America is well documented and the reasons for its decline are understood (see Sykes 1984), the change in the breeding distribution of the swallow-tailed kite over the last century has never been adequately explained. This becomes even more perplexing when one considers

the currently expanding ranges of the two remaining North American kites: black-shouldered kite (*Elanus leucurus*) and Mississippi kite (*Ictinia mississippiensis*) (Palmer 1988). Furthermore, the latter species occupies habitats similar to those of the swallow-tailed kite in the Southeast.

Although general accounts cite habitat destruction, over-collecting of eggs, and shooting adult birds as primary reasons for the disappearance of the species from the northern portion of its range, this is not documented. The limited amount of existing museum material does not support the contention that over-collecting occurred. Additionally, not only is the diet opportunistic, but also the nesting habitat discussed for former northern populations by various authors (see Bent 1937) does not seem restrictive. The general disappearance at the turn of the century from northern nesting sites was well before the invention of persistent pesticides, and our preliminary evidence on natural mercury loads suggests that the species' position in the food chain would not make it particularly vulnerable to human-induced contaminants.

Historical records indicate that the upper Mississippi basin population was much larger, and probably more uniformly distributed, than the scattered records indicate. For example, Simpson (1972) records that swallow-tailed kites were regular late summer visitors in the mountains of North Carolina during the 1800s and had almost disappeared by 1900. Simpson attributed this loss to the shrinkage in the breeding range and believed that the fall migrants were from the breeding population in the upper midwest that were moving east and south down through the Appalachians. Loomis (1890) noted a similar situation in the mountains of South Carolina. Nevertheless, this may not be the case, and in the north the species may have been restricted to only a small number of relict breeding sites in the historical period.

*Phenology*—Millsap (1987) reported on massive pre-migration staging at a site near Lake Okeechobee, Florida, where he observed large numbers of kites in communal roosts from mid-July through mid-August. Monitoring the following year provided additional data (Millsap and Runde 1988). The roost he described was used by at least 1,339 kites on 7 August 1987, and the kites used the roost from 12 July to 1 September 1988. The numbers of kites in the Okeechobee roost, those in other communal roosts reported on by Millsap and Runde (1988), and historical information on summer flocks (1924–82) of swallow-tailed kites in the same general area (Millsap 1987) suggest that the low population estimates of swallow-tailed kites from the late 1970s may have been underestimates. As of



1985, the species is a Category 2 candidate for federal listing as a threatened or endangered species (United States Fish and Wildlife Service 1985).

Whether our observations and collections represent another roosting area for pre-migration staging or simply a gathering of local post-nesting birds is unknown. No mention of molt is made in the summer roosting flocks reported to date (Millsap 1987, Millsap and Runde 1988). Because of this and the general lack of young birds in our study area in early July, we theorize that after the nesting season (mid-March through late June) local adult birds gather in small flocks, forage, build up pre-migratory subcutaneous fat reserves, and complete their flight feather molt (July). They undergo short distance movements (late June and August with a peak in early July) to larger communal summer roosts that are adjacent to extensive foraging areas. The appearance of numbers of birds at communal roosts in early to late July may represent immature birds that do not undergo molt. The subsequent build up in early August would then result from adults coming to the roost after molt was completed. From mid-August to early September, the kites depart for wintering grounds in South America (Brown and Amadon 1968, Robertson 1988); the south Florida birds take a trans-Caribbean or trans-Gulf migration route (Millsap 1987).

### CONCLUSION

The American swallow-tailed kite is currently regarded as a "Category 2" species under the Endangered Species Act, meaning that not enough is known about its status to list it as Threatened or Endangered. There is documentation showing an overall decline in the breeding range during the historical period, but in most regions this documentation is less than adequate. Furthermore, the generalized diet and the fact that the kite feeds low on the food chain combined with the nonspecific habitat requirements confound efforts to determine reasons for the decline. Its disappearance from northern nesting sites was long before persistent pesticides were introduced in the environment. Over-collecting of eggs and shooting of adult birds has often been cited as the primary reason for the disappearance of the species from portions of its breeding range, but there is no evidence that this is the case.

Our documentation of the molt period of adults will allow field workers who monitor summer populations to obtain much needed information on age ratios and post-breeding movements of different age classes. This information should prove useful in determining the conservation status of this kite.

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First Specimen of the Shiny Cowbird,  
*Molothrus bonariensis* (Aves: Emberizidae),  
in North Carolina

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**ABSTRACT**—The first North Carolina specimen of the shiny cowbird (*Molothrus bonariensis*), representing the fourth collected in North America, was obtained at New Bern, Craven County, in 1990.

Since about 1900, the shiny cowbird has been spreading northward through the West Indies at an accelerating pace (Post and Wiley 1977, Post et al. 1992). This species was first sighted in North America, on the Florida Keys, in 1985 (Smith and Sprunt 1987). It was photographed on the Florida mainland in 1987 (Smith and Sprunt 1987). Since it was first noted on the mainland of North America, the shiny cowbird has spread throughout Florida, particularly south of Tampa (Post et al. 1992). Individual cowbirds have begun to make long-range movements from the Florida population center, reaching as far northwest as Oklahoma (Grzybowski and Fazio 1991) and northeast to Maine (Turner 1992).

As yet, only a few shiny cowbirds have been collected in North America. The first North American specimen was obtained in 1989 in South Carolina (Hutcheson and Post 1990). The second and third were obtained in 1990, in Texas (G. D. Baumgardner, Texas A & M University, *in litt.*) and in Oklahoma (Grzybowski and Fazio 1991), respectively.

The fourth North American specimen, and the first for North Carolina, was obtained by Robert P. Holmes, III at New Bern, Craven County, on 29 October 1990. The specimen is an adult (after second-year) male (USNM No. 597,185). The skull was fully pneumatized. Testes measurements were left: 1.5 x 1.5 mm and right: 1.0 x 1.0 mm. The bird had no subcutaneous fat. Mass was not recorded. The flattened wing length (wrist to tip of longest primary) was 100.0 mm. The wing molt was completed. The bird was still undergoing a slight body molt in the region of the malars and upper breast. By comparison with specimens in the Charleston Museum, I determined that the individual belongs to the subspecies *M. b. minimus*.

Besides being the first specimen for North Carolina, this also appears to be the first verifiable record for the state. The species

was reported from North Carolina in 1989, and that report was accompanied by a photograph (Cooper 1990). Although the observer meticulously recorded the details of his observation, and the report is undoubtedly correct, the photograph itself is not clear enough to exclude the possibility that the individual is a brown-headed cowbird (*Molothrus ater*).

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## ERRATA

Joshua Laerm has informed the editor of an error in *Brimleyana* 18. On page 23 of "A Late Pleistocene Vertebrate Assembly from the St. Marks River, Wakulla County, Florida," the sentence beginning on line 7 should read: "Two species of rabbit occur in the St. Marks region today, the eastern cottontail, *Sylvilagus floridanus*, and the more common marsh rabbit, *S. palustris*." The swamp rabbit, *S. aquaticus*, is not known to occur in Wakulla County, Florida.



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